EFFECTS OF GAZE POSITION ON TOUCH LOCALIZATION

LISA MARIE PRITCHETT

A DISSERTATION SUBMITTED TO
THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN PSYCHOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO

April 2016

Abstract

Previous research has shown that the direction of gaze relative to the body affects the perceived location of touch, and has argued that these effects indicate that a gaze-centered reference frame is used for touch localization. In this dissertation I examine a discrepancy in the existing literature: why do different studies report opposite directions of effects when eye and head positions are manipulated separately? I resolve this discrepancy by showing that it is not due to whether eye or head position is manipulated (chapter 2) but is in fact due to the nature of the task (chapter 3). I also find that the effect occurs on the back of the body (chapter 4), a body part that is not normally in view and thus would be less likely to use gaze as a reference point. I test theories for why these effects occur (chapter 5), and find that results are compatible with the perceived location of a touch being attracted towards the location of gaze, at least for perceptual measures. When location was reported by pointing, an action-based measure, I find no effect of gaze direction on touch localization, suggesting that a gaze-independent reference frame is used for action. These behavioral results are complementary to recent neurophysiological and neuroimaging findings indicating that spatial locations are coded in a range of different reference frames, and indicate that gaze-related reference frames are behaviorally relevant in tactile localization.

Acknowledgements

Completion of this dissertation is a huge accomplishment. There were definite times when I did not think it would ever happen. The support from those around me has certainly made the difference. First and foremost I must thank my supervisor Laurence Harris. From the first day I met him on interview in February of 2009 his enthusiasm for studying sensory perception has been a huge motivator for me. Laurence has been a superb supervisor. This dissertation would not have been possible without him. I would also like to thank my PhD committee members, Doug Crawford and Joe DeSouza; thank you for your always helpful comments, corrections, and questions; as well as David Shore for careful review and editing of the final version.

I would also like to thank the other students in the Harris lab. Vanessa Harrar completed her PhD within the first semester I was enrolled at York University. As they say, scientists stand on the shoulders of the giants, and in my case it is Vanessa's shoulders I stand on (amongst others). Even after Vanessa left York to continue her academic career, discussions with her online and at conferences have been a huge influence on my work. Next I must thank Michael Carnevale whom started as an undergraduate thesis student, and continued on to complete a Master's degree in our lab. Michael spent several years working directly with me and he coauthored Chapter 3 in this dissertation. Michael loved to discuss science and conversations with him had a large impact on the ideas described in this dissertation. Finally I must thank all of the students who have come and gone through the Harris lab in the 6+ years I have been a part of it. Thank you Adria Hoover, Blake Martin, Ryan Dearing, Charles Mander, Sarah D'Amour, Lindsey Fraser, Meagan McManus, Stefania Moro, Yasmeenah Elzein, and Bobbak Elm. I would also like to thank my best friend MInjung Kim for all of her support in the time since we both moved to Toronto. Good luck to her as she completes her PhD this summer as well!

Finally I would like to thank my family for their support through the past years. In particular, I must thank my parents, David Pritchett and Janice Miller Russell, both of whom passed away in the time I have been a PhD student. My parents both supported and encouraged me through my education. They were so proud of me, and I wish they could see me on the day I defend my dissertation or the day I receive my PhD degree. It has been their passing that has made completing my degree the most challenging, but also their memory that encouraged me to never give up. I would like to thank my brother Andrew and sister Holly, as well as my Aunts and Uncles. Also I must thank my mother-in-law, Irene Tudoir, and father-in-law, Josef Sarniak, and brother and sister in-laws Robin and Sandra who have accepted me whole-heartedly into their family.

To my partner, Darren Sarniak, you have been the best thing in my life for 5 years. More than anyone, you have helped me to move through the challenges. I love and cherish every day I am lucky enough to have a portion of it with you. And finally, to my unborn child who is kicking in my tummy at the moment I write this: your (not so) tiny kicks have been a huge motivator to finish this thing off (I am 37 weeks pregnant today, the day I finally submit this final version).

Thank you all.

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Chapter 1. General Introduction

We perceive multisensory space all around us. It is remarkable that this perception is supported by our senses when we consider the limited window into the world that each sense provides. Visual information is initially available from photoreceptors that provide a topographic map of the visual field of each eye, so that spatial visual information is initially provided in an eye-centered reference frame. If the location of an object sensed through vision is needed to be known relative to the body, the orientation of the eyes in the head and of the head on the body (i.e., gaze: the orientation of the eyes relative to the body) would be needed. Similarly, objects coming into contact with the skin trigger mechanoreceptors, which provide a map of the surface of the skin, just as the retina provides a map of visual space. Tactile information is thus initially available in a skin-centered reference frame. To code the location of a tactile stimulus in an eye-centered reference would require information about the position of the relevant body part relative to the eye, including the relative positions of the eyes, head, and the body part. Each of these components (eye, head, trunk, each body part and external space) provides a potential reference frame (i.e., a known location with which to record a location relative to). Figure 1.1 illustrates several possible reference frames that could be used to code the location of a tactile stimulus.

The fact that we are able to reach toward visual stimuli and move our eyes toward tactile stimuli proves that we are able to transform between these reference frames. When we reach to a visual stimulus we have taken the location of an object whose location is known based on the location of light on the retina and determined its location relative to our body. Similarly, when we move our eyes to a tactile stimulus we have taken its location, initially available as a location of skin on the body, and determined how that location compares to the current position of our gaze. Both of these examples require reference frame transformations, but how the transformations are accomplished is a topic of much ongoing debate. It used to be believed that the primary sensory cortical areas coded stimulus location in the native reference frame for that sense (i.e., eye-centered for vision and body-centered for touch) and that multisensory areas coded stimuli in a single common reference frame (e.g., Stein & Meredith, 1993). However, more recently it has become evident that multisensory brain areas can simultaneously code stimuli locations in multiple reference frames (Duhamel, Bremmer, BenHamed, & Graf, 1997). The picture emerging is of a highly flexible system where a location initially coded in the native reference frame of that sense is immediately transformed into a continuum of other reference frames (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005).

In this thesis, I will describe several experiments where gaze is manipulated relative to the body in order to separate gaze and body related reference frames while tactile stimuli are applied to the skin surface. I will examine how location estimates of the tactile stimulus are affected by the angle of gaze and reveal details of the reference frames in which they are coded. Before describing my experiments in more detail, I will review what is already known about how the brain solves the multiple reference-frame problem. I will begin with a general review of how touch location is initially coded in the brain, starting with the mechanoreceptors in the skin and ending with different representations of that location in the cortex. I will then review a large literature that has already examined effects of gaze direction on the perception of location and on actions directed toward those locations, and identify areas where I can contribute by filling in gaps in current understanding. Finally, I will describe the behavioral experiments I have conducted, which will help to elucidate the coding mechanisms that are used in tactile localization.

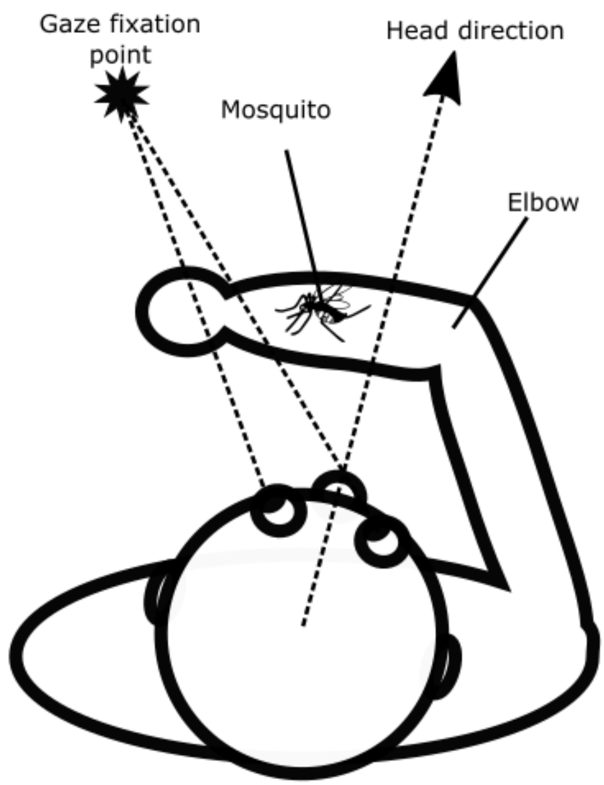

Figure 1.1. A tactile stimulus, such as a mosquito landing on one's arm, can be localized in many different reference frames. It initially stimulates receptors in the skin providing a signal to the brain for the part of skin the mosquito landed on. That location could then be described in a body-centered reference frame, such as relative to the elbow, or in a head-centered reference frame relative to the direction of the head, or in a gaze-centered reference frame relative to the direction of gaze.

Neuroscience of Touch

Mechanoreceptors and Initial Pathways

When a tactile stimulus is applied to the skin, the mechanoreceptors embedded within that local area of the skin are stimulated. There are several different types of mechanoreceptors which can be classified by the size of their receptive fields (the area within which they will respond to stimuli), and by the adaption rate (how long after a stimulus is applied that the receptor will continue to respond) (Bolanowski, Gescheider, Verrillo, & Checkosky, 1988). Mechanoreceptors with large receptive fields are embedded deeper in the skin, causing them to respond to stimuli from a larger area, whereas those that are closer to the surface have smaller receptive fields.

In the experiments described in this thesis several of these receptor types are involved. In Chapter 2 a blunt solenoid is applied to the skin, causing pressure and skin stretch at that location, which would be detected by the slowly adapting, small receptive field Merkel disk receptors. These respond as long as the stimulus is applied. The solenoids would also stimulate the rapidly adapting Meissner corpuscles, which would respond when the stimulus was first applied and again when it was removed. In the experiments described in Chapter 3 through Chapter 5 a vibration stimulus is applied to the torso, which would be primarily detected by the very rapidly adapting Pacinian corpuscle receptors featuring large receptive fields, located deeper in the skin. The vibration frequency 250 Hz was chosen because that is the peak sensitivity for the Pacinian corpuscle (Talbot & Mountcastle, 1968).

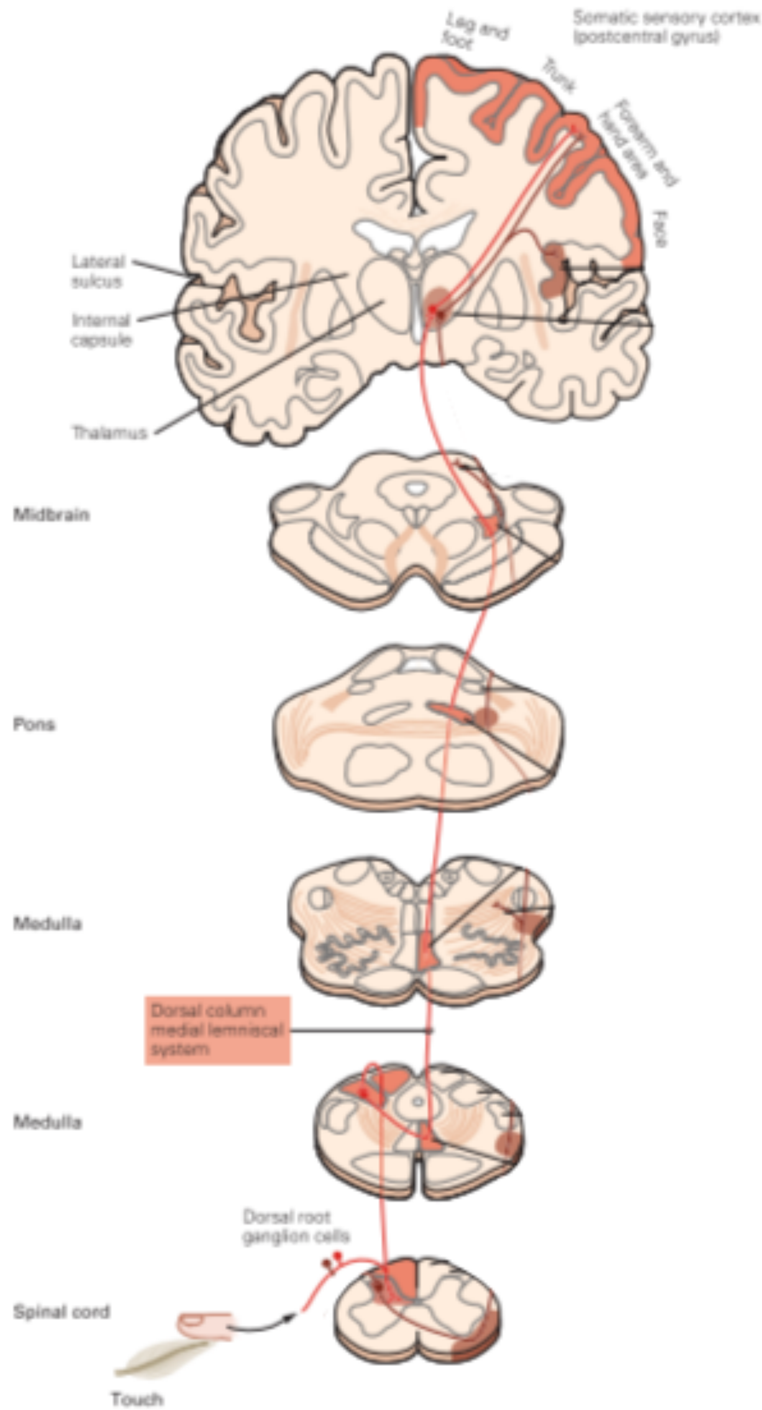

Figure 1.2. Tactile sensory pathway. Mechanoreceptors, which are neurons with receptors in the skin have their first synapse at the dorsal root ganglion cells in the spinal cord. Signals are then sent through the brainstem (medulla and pons), the midbrain, and the thalamus, before reaching the primary somatosensory area in the postcentral gyrus. Image adapted from Kandel, Schwartz, Jessell, Sigelbaum, and Hudspeth (2013, fig 22-11, p. 492-493).

The density of receptors in the skin is not constant, but depends on the part of the body stimulated. The skin on the fingertips and mouth are the most important for exploring the world, and thus contain the largest density of receptors. In contrast, the trunk is rarely used for tactile exploration of the world, so it has comparatively few receptors.

Regardless of the mechanoreceptors that initially transduce a tactile stimulus, nerve fibers from all the receptors in a given region of skin are bundled with fibers from proprioceptive receptors in the muscles and joints, and have their first synapse at the dorsal root ganglia. Signals (except those from the face) then enter the spinal cord through spinal nerves. These signals are then transmitted through the brainstem (the medulla and pons), the midbrain, and the thalamus to the Primary Somatosensory Cortex (SI). Throughout this relay of information a somatotopic organization is preserved. An illustration of the tactile pathway appears in Figure 1.2.

Superior Colliculus

The superior colliculus (SC) is a midbrain structure that controls automatic orienting of the eyes, head, and body towards unexpected stimuli, and receives sensory information independent from the pathways taking information to the cortex. The superficial layers of the SC contain cells responsive to visual stimuli that are organized in a retinotopic map. In deeper layers of the SC the cells also respond to auditory and somatosensory stimuli (Schiller & Stryker, 1972; Stein & Meredith, 1993). Interestingly, the organization of those multisensory cells are retinotopic;

auditory (Hartline, Pandey Vimal, King, Kurylo, & Northmore, 1995; Martha F. Jay & Sparks, 1984; Peck, Baro, & Warder, 1995) and somatosensory (Groh & Sparks, 1996) receptive fields shift with changes in eye-position. This means that the part of skin that is represented by a deep somatosensory cell in the SC will depend on eye position. This sort of eye-position dependent response in the SC could cause systematic errors in sensory localization of auditory and somatosensory stimuli, especially if the receptive fields only shift partially with eye position, as has been found (Hartline et al., 1995; Jay & Sparks, 1987; Jay & Sparks, 1984).

Primary Somatosensory Cortex

S1 comprises Brodmann cortical areas 3a, 3b, 1, and 2. Areas 3a and 2 are the projections for proprioceptive information, while areas 3b and 1 are the primary tactile areas. Areas 3a and 3b receive input directly from the thalamus and relay it to areas 1 and 2. Each of these areas contains a separate and distinct somatotopically organized map of the body.

The somatotopic organization of SI was shown in groundbreaking studies by Penfield & Boldrey (1937). They directly stimulated brain regions of patients undergoing brain surgery and recorded what parts of the body the patient felt an illusion of stimulation. Their work demonstrated several important concepts. First, SI is organized somatotopically, and second, that the size of brain regions associated with each part of skin is not constant, but depends on the density of receptors. Thus, areas with the largest number of receptors in the skin (the finger tips and mouth) also have the largest areas of SI associated with them. These findings are illustrated by the somatotopic mapping and homunculus drawn in Figure 1.3.

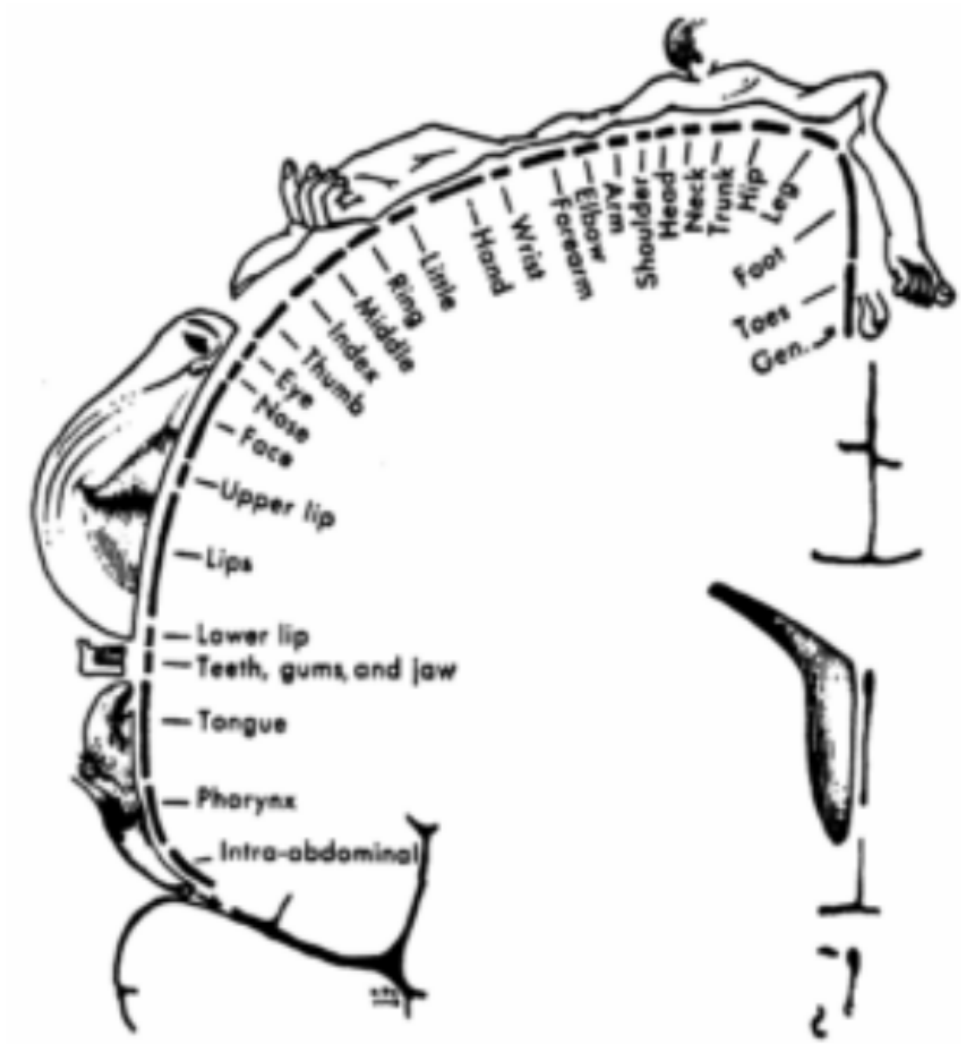

Figure 1.3. Somatotopic mapping of Primary Somatosensory Cortex). Image adapted from Penfield and Rasmussen (1957, fig 114, pp 214-215).

Dorsal and Ventral Pathways from SI

After processing in SI, tactile information is processed along two parallel pathways (Reed, Klatzky, & Halgren, 2005), similar to how vision in processed (Goodale & Milner, 1992). In vision, one path, known as the ventral ("what") pathway, is involved in identification by processing features such as size, intensity, and shape and involves memory to recognize an object. The other pathway, the dorsal ("where") pathway, processes location information and connects to the motor areas to direct action. This "where" or "action" pathway is most important here, though the two pathways do communicate (Goodale, 2011).

Along the "what" pathway in the somatosensory system, information is relayed to the Secondary Somatosensory Cortex (SII), which is necessary for object identification and processes shape, texture, and temporal information. SII sends and receive information from the Premotor and Prefrontal area, and has connections the hippocampus to draw on memories (Reed et al., 2005).

Along the "where" pathway in the somatosensory system, SI sends information directly to the Posterior Parietal Cortex (PPC) and the Primary Motor Cortex (MI). The posterior parietal cortex integrates information from many sensory systems, and is the brain region most likely involved in the gaze related errors that are to be reported here.

Posterior Parietal Cortex

The PPC receives projections from primary, visual, auditory, vestibular, and somatosensory areas, as well as from efferent motor pathways (Andersen, Asanuma, Essick, & Siegel, 1990). As such, the PPC has long been considered an association area where a single perception of space is constructed by combining sensory and motor information (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). Patients who have had lesions to the PPC exhibit spatial neglect where they ignore the side of space opposite to the lesion (Bisiach, Cornacchia, Sterzi, & Vallar, 1984). This deficit is seen in all sensory modalities and can be observed relative to several reference frames, including eye-, head-, body-, and environment centered. Deficits are seen for all actions towards that part of space (Pizzamiglio et al., 1989). These effects point to the multisensory nature and multiple reference frames used in the parietal cortex.

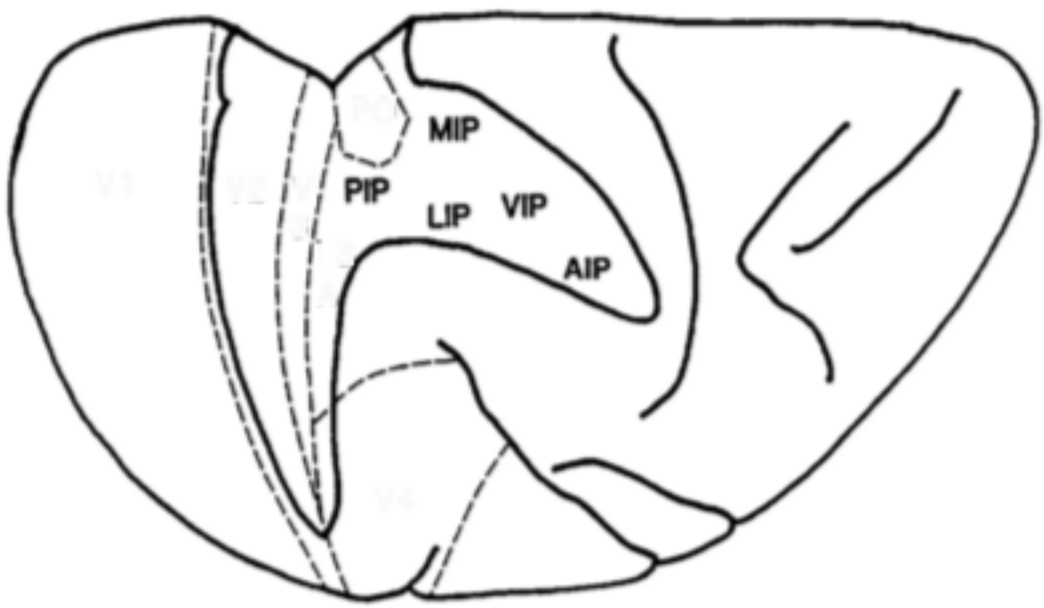

Figure 1.4. Functionally defined regions in the posterior parietal cortex of the macque. PIP, the posterior intraparietal area; MIP, the medial intraparietal area; LIP, the lateral intraparietal area; VIP, the ventral intraparietal area; and AIP the anterior intraparietal area. Adapted from Colby, Gattass, Olson, and Gross (1988, fig. 1, p. 394).

The PPC can be further divided into many subareas, defined by the type of stimulation each responds to optimally. Some of the regions identified in the macque monkey are illustrated in Figure 1.4. The PPC has been extensively studied using single-unit electrical recording of neurons in the monkey (for reviews, see

Andersen, Snyder, Bradley, & Xing, 1997; Colby & Goldberg, 1999; Colby, 1998). These studies have indicated that different subregions are specialized to guide different types of actions. One of the best studied, the Lateral Intraparietal (LIP) area, seems to be specialized to guide saccades. It is primarily activated by visual stimulation, but stimuli in other modalities can also evoke activity if an eye movement is to be made towards it (Mazzoni, Bracewell, Barash, & Andersen, 1996). In contrast, the ventral intraparietal area (VIP) is particularly responsive to tactile stimulation, especially to the face and mouth, but is also responsive to visual stimuli near the head. This area seems to be specialized for reaching with the head and mouth towards ultra-near stimuli. As the name suggests, the parietal reach region (PRR) is specialized for arm and hand movements toward stimuli of any modality within reaching distance.

Effects of Gaze Position on Sensory Responses in the Cortex

Neurons in the PPC exhibit spatially selective receptive fields. That is, they fire in response to stimuli in given locations. Locations can be defined in many different reference frames. For example, LIP neurons exhibit eye-centered reference frames, meaning that a location must be at a set location relative to the fovea in order to cause a neuron to fire. However, the actual rate a neuron fires in LIP is not only dependent on the location of the stimulus relative to the fovea, but also on the orientation of the eyes in the head. Andersen and Mountcastle (1983) first described this “gain field” effect, whereby the firing rate of a neuron in the PPC depends on the orientation of the eyes in the head even given the fixed retinotopic receptive field of the neuron. Figure 1.5 Illustrates a neuron with a retinotopically defined receptive field and an eye-position gain field. Subsequently, Andersen, Essick, and Siegel (1985) reported that these gain-fields could be used to compute a head-centered representation of the location of a stimulus. That means that even though the neuron's receptive fields are in eye-centered coordinates, if the response of a population of cells were examined concurrently a head-centered location could be deduced as only a subset of neurons that were selective for a given eye position would be active. Further, when a neural network was trained to transform signals from eye- to head-centered coordinates it spontaneously developed eye-position gain field like behaviour (Zipser & Andersen, 1988). Thus, eye position gain fields in PPC are likely involved in spatial transformations between reference frames. Gain fields do not only exist for eye position; head position gain fields have also been found by Brotchie, Andersen, Snyder, and Goodman (1995), who found that both eye and head position provided the same gain-field behaviour, and concluded that gain modulation is probably dependent on gaze direction (where gaze = eye + head relative to space), rather than as separate eye and head effects. Gain field modulation has also been described depending on the orientation of the body relative to space in area 7a (Snyder, Grieve, Brotchie, & Andersen, 1998), and depending on the distance between the hand and the location of fixation in the PRR (Chang & Snyder, 2010).

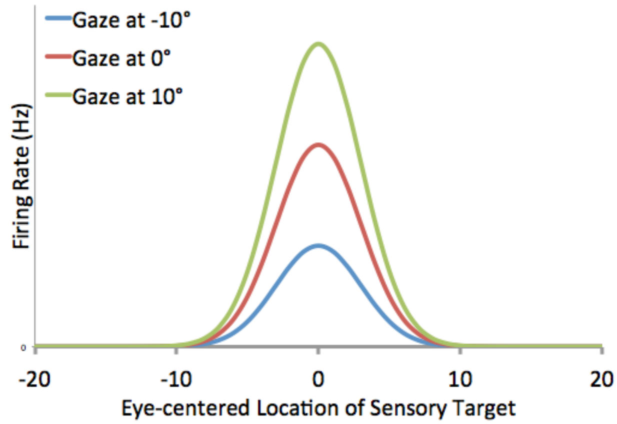

Figure 1.5. Response of a hypothetical neuron with a retinotopic receptive field and eye position gain fields preferring eye-positions to the right (positive).

Gain fields are one mechanism in the PPC by which locations in multiple reference frames can be achieved simultaneously. In addition, individual neurons in PPC have receptive fields defined in many different reference frames. For example, LIP neurons that respond to auditory stimuli were found to have both eye- and head-centered receptive fields, as well as receptive fields that were somewhere between eye- and head-centered (Stricanne, Andersen, & Mazzoni, 1996). Examples of the response pattern of neurons coding in eye, head, and intermediate coordinates are illustrated in Figure 1.6. Similar results have been found for visual neurons in area VIP (Duhamel et al., 1997), but tactile receptive fields in VIP appear to code location only in head or body-centered coordinates, and were not found in intermediate or eye-centered coordinates (Avillac et al., 2005). Though eye-centered receptive fields were not found for tactile neurons in VIP, these neurons still exhibit gaze-related gain fields, so a gaze-centered representation of touch locations may still be available (Avillac et al., 2005).

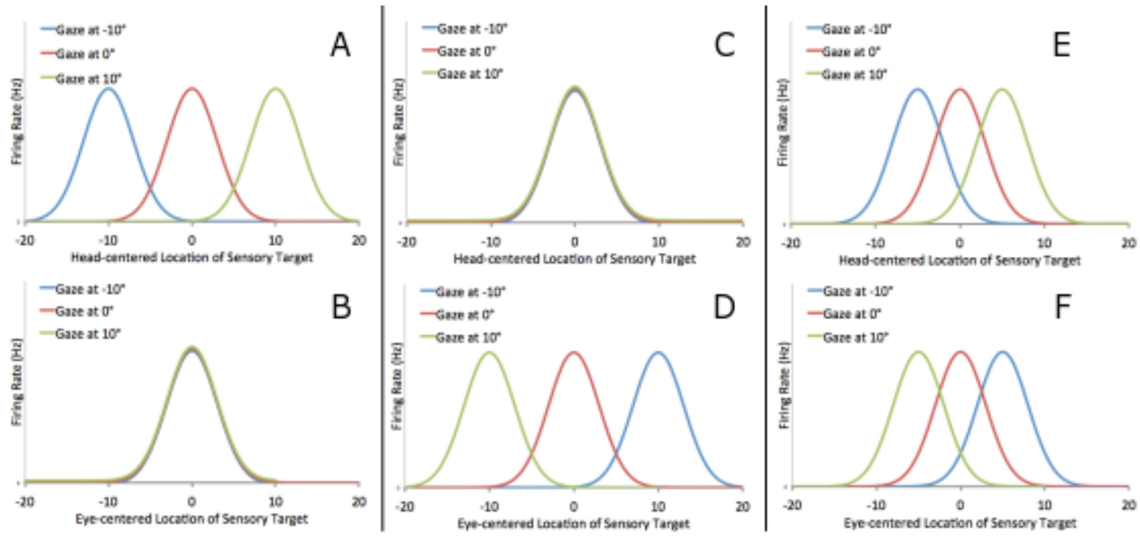

Figure 1.6. Example of neural responses from hypothetical neurons coding in eye-centered (A and B), head-centered (C and D), and intermediate coordinates (E and F), plotted as a function of either head-centered or eye-centered location of sensory target. Adapted from Cohen and Andersen, (2002, fig 2, p. 555).

These gain-fields and neurons coding in a continuum of reference frames have been shown using single unit recording of neurons in monkeys. Functional magnetic resonance imaging (fMRI) has suggested that similar effects are found in the human PPC (DeSouza et al., 2000; Medendorp, Goltz, Vilis, & Crawford, 2003). Sereno and Huang (2006) reported an area similar to monkey VIP (a homologue). Just as was found with monkeys, this area coded visual locations in eye, body, and intermediate reference frames, while tactile location seemed to be only in a body-centered reference frame. However, Buchholz, Jensen, and Medendorp (2013) reported that tactile evoked MEG oscillatory activity in VIP was affected by gaze-direction, suggesting that body and gaze-centered representations may be communicated in different temporal patterns, which would be invisible in fMRI. This suggests that neurons in human VIP may well code tactile locations in both body-centered and gaze-centered reference frames.

Finally, there is at least one report of eye position affecting the response properties of neurons in the primary somatosensory cortex, which, as already described, is organized in a somatotopic map. Forster & Eimer (2005a) found that tactile evoked ERPs, believed to originate from the primary somatosensory cortex, are modulated by gazing towards the touch location. Furthermore, the effect of gaze direction on tactile ERPs was independent from the effect of viewing the body part touched. Vision of the stimulated hand caused enhancements to early components (the P45 and N80) whereas gazing towards the hand while the hand was occluded from view caused enhancements to later components (the N140 and later), without affecting the earlier components. The authors argue that these results indicate that vision and gaze direction modulate tactile processing in S1, likely due to feedback from the PPC.

The research reviewed here indicates that the direction of gaze affects the neural processing of touch locations. Touch locations may be available in a variety of reference frames, including eye-centered, in addition to the initial somatotopic locations provided from receptors in the skin. Are these representations of location actually used in spatial perception and action? To determine the relevance of these neurological findings for perception and action behavioral research must be carried out. In the next section I review previously reported effects of gaze direction on spatial perception and action.

Effects of Gaze Direction on Perception and Action

The earliest report of gaze direction affecting spatial perception was by Delage (1886) who reported that if a person stands against the wall with their head turned hard to the right and is asked to direct a pointer straight ahead relative to their body he will actually point about 15 degrees to the left (cited in Pierce, 1901). Since then, a very large literature examining effects of gaze direction on spatial perception and action has emerged. Here I will review effects of gaze direction on perceived locations of auditory, visual, proprioceptive, and finally (the topic of this thesis) tactile stimuli.

Effects of Gaze Direction on Auditory Localization

In the earliest report about gaze direction on auditory localization (Pierce, 1901) found that the location corresponding to the auditory zero (straight ahead, or equally left and right) was shifted in the same direction as an eccentrically positioned head. This indicated that the perceived location of sounds was shifted in the direction opposite to head position. In contrast, displacing the eyes caused the opposite pattern of results: the auditory zero-point shifted in the opposite direction as the eyes, indicating a shift in sound localization to the same direction as the eyes. That eye position shifts sound localization in the same direction as the eyes was also found by Weerts and Thurlow (1971); however, Ryan and Schehr (1941) found that eye eccentricity affected sound localization differently for different participants.

More recently, Lewald and colleagues have published a series of studies to clarify the effects of eye and head position on the perceived location of sound

(Lewald, Dörrscheidt, & Ehrenstein, 2000; Lewald, Karnath, & Ehrenstein, 1999; Lewald & Ehrenstein, 1996a, 1996b, 1998, 2001; Lewald, 1997, 1998). In their first report, (Lewald & Ehrenstein, 1996b) they manipulated eye position and presented dichotic sounds (tones presented over headphones with differing intensity levels to the left and right ear, leading to the perception of a single sound inside the head whose location depends on the relative intensity of the sounds presented to each ear) . Participants either adjusted the left-right balance of the sound such that it was perceived at the median plane of the head, or else they compared the location of the sound to the median plane of the head in a forced-choice task. In either case they found that the perceived median plane shifted in the same direction as the eye position, indicating sound location shifted in the opposite direction as eye position. In their next report (Lewald & Ehrenstein, 1996a) participants compared the location of externally presented sounds to a visual reference point while eye position was manipulated. Eye position shifted the perceived location of sounds in the same direction as eye position, but argued that the visual reference was probably affected more than the auditory stimulus, and concluded that both visual and auditory locations were shifted in the opposite direction to eye position. The same data from Lewald and Ehrenstein (1996a) also appears as the first experiment in Lewald (1997). In addition, Lewald (1997) reported that if no visual reference point were provided and participants were asked to report the location of a sound relative to the perceived straight-ahead (i.e., relative to the head), different participants showed different effects, perhaps indicating differing strategies adopted by the participants. The hypothesis from Lewald and Ehrenstein (1996a) and Lewald (1997) that both visual and auditory locations are shifted in the opposite direction as eye position but by different amounts was tested and confirmed by Lewald (1998), where participants pointed towards both visual and auditory targets while the eyes were held eccentric. In the next series of experiments (Lewald et al., 2000, 1999; Lewald & Ehrenstein, 1998), they examined the effect of head position on perceived sound localization. They found that head position affected sounds similarly to the way eye position did for both dichotic sounds perceived inside the head (Lewald & Ehrenstein, 1998), and virtual sounds that are perceived as external (Lewald et al., 2000). In addition they found that illusory head turns from vibrating the neck muscles also causes the effect (Lewald et al., 1999), suggesting that neck proprioceptive input is used. Finally, Lewald and Ehrenstein (2001) examined effects of eye position on sounds in the rear space in a task where participants compared the location to the median plane. The perceived median plane shifted in the same direction as gaze, indicating sounds were shifted in the opposite direction, consistent with their previous findings. Throughout this literature Lewald and colleagues speculate that these effects of gaze direction on sound localization reflect reference-frame transformations for sound where the initial head-centered representation of sound is transformed to eye-centered or body-centered representations, probably within the superior colliculus or posterior parietal cortex.

Effects of Gaze Direction on Visual Localization

The direction of gaze has also been found to affect the perceived location of visual targets. Hill (1972) examined a curious effect that a light appeared to jump in space during an eye movement. He reasoned that the effect could be due to an error in how the brain processes the location of gaze: if the signal for gaze location in the brain were underestimated, the perception of the straight ahead direction would be shifted toward gaze position and visual locations would be perceived as shifted in the opposite direction. Conversely, the effect could be due to misinterpreting the external location associated with the stimulated location on the retina. To investigate, Hill (1972) conducted an experiment where participants adjusted a light to their perceived straight-ahead while their eyes were positioned eccentrically. Perceived straight ahead was consistently underestimated (shifted towards gaze position). If the errors in perceived direction were due to an underestimated representation of gaze location then the perceived locations of visual stimuli perceived foveally with an eccentric eye position should show errors (as in Figure 1.7A), but locations viewed in the periphery while gaze was centered should not show errors (as in Figure 1.7B). In contrast, if the errors in perceived direction were due to errors in retinal location then the opposite pattern should be observed: errors would be related to peripherally viewed targets with gaze centered (7B) but not foveally viewed targets with gaze eccentric (7A). His results suggested that the errors in perceived visual direction were due to an underestimated representation of gaze and not errors in perceiving retinal location.

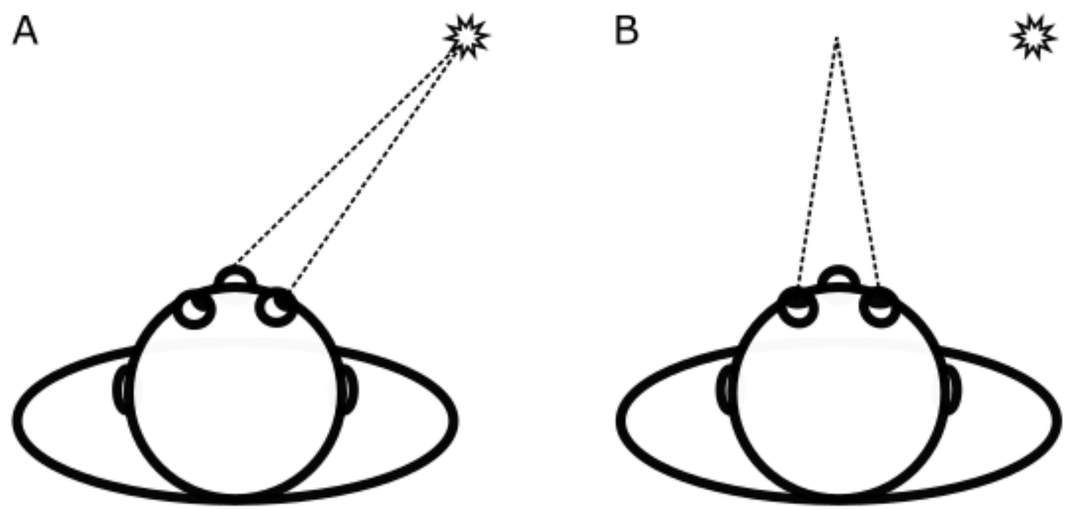

Figure 1.7. If the effect of eccentric gaze on perceptual localization were due to an underestimated representation of gaze there should be perceptual error in A where gaze direction is eccentric but not in B where gaze direction is centered on the body. If the effect is due to misperceiving the retinal location there should be perceptual error in B where the stimulus is in the periphery on the retina, but not in A where the stimulus falls on the fovea.

Although results from Hill (1972) suggest that errors in visual perception are related to an underestimated representation of gaze, further research has contradicted these results. Morgan (1978) and Yamaguchi and Kaneko (2007) conducted experiments with a similar rationalization and procedure and found that both underestimated representation of gaze and retinal localization errors caused errors in perceived visual location. In addition, results from Bock (1986) completely contradict Hill's (1972) findings. Bock (1986) found that when pointing towards visual targets which were viewed foveally with eccentrically positioned gaze (as in 7B) there were consistent overshoots. However, when targets were viewed foveally but with gaze at 30 deg left relative to the body midline (as in 7A), pointing was accurate. This pattern of effects suggests that the errors are not due to errors in the perceived location of gaze on the body, but instead caused by a misperception in the external location of visual stimuli associated with the peripheral retina, specifically perceiving the location of peripherally viewed visual stimuli as more eccentric than they actually are. Bock referred to this as the "retinal magnification effect" (RME). His conclusion that effects of gaze direction on visual target localization are due to the RME has not been universally accepted, however. Recently, McGuire and Sabes (2009) concluded that the effects could still be due an internal estimate of gaze direction being biased towards the location of a visual target, similar to Hill's (1972) conclusion that the internal estimate of gaze angle is underestimated (similar at least in conditions where gaze is eccentric and target location is centered). In addition, since studies supporting the RME theory usually measure localization by pointing or reaching, the RME could be a result of misperceiving the location not of the visual stimulus itself but of the hand used in reaching to the visual target. Dessing, Byrne, Abadeh, and Crawford (2012) found that, if the location of the reaching arm was always visually available, the RME disappeared.

In contrast to the reports of the RME where visual locations are perceived as *further* from the fovea than they actually are, a separate body of literature has consistently found that briefly presented visual stimuli are perceived as *closer* to the fovea than they actually are, a phenomenon known as "foveal bias" (Eggert, Ditterich, & Straube, 2001; Kerzel, 2002; Mateeff & Gourevich, 1983; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999). In these studies, eye position is generally not manipulated, and instead is held central while peripheral stimuli are briefly flashed. Whether the retinal magnification effect (errors away from the fovea) or foveal bias (errors toward the fovea) are found may depend on the duration of the stimulus presentation and/or the method of localization: foveal bias is found specifically for stimuli presented for very brief periods (i.e., less than 300 ms) and are perceptually located (e.g., relative to a scale), while in studies finding the RME, target presentation is for at least 700 ms and stimuli are localized by pointing or reaching.

Henriques, Klier, Smith, Lowy, and Crawford (1998) exploited the RME to examine whether visual pointing targets are updated in a gaze-centered or body-centered reference frame. When a visual target is viewed foveally, its location could be coded in a body-centered reference frame for a subsequent pointing response. This would seem more likely than the visual target location being updated in a gaze-centered reference frame, which would require updating its location whenever gaze moved relative to the body. Further, pointing movements do not require gaze information, they are entirely body-centered, so a gaze centered updating scheme seemed quite unlikely. Neurophysiological findings at the time were suggesting that a gaze-centered reference frame may be used for pointing (see next section), so Henriques et al, (1998) set out to test for gaze-centered updating in a behavioral paradigm. Participants viewed a central target foveally, and then moved their gaze to an eccentric position before pointing to the remembered location of the target. Surprisingly, the same pointing overshoots were found in this condition as when the target was only viewed peripherally (as in Bock, 1986, and replicated in Henriques et al., 1998). This observation indicated that the visual target was indeed updated in a gaze-centered reference frame. In a control experiment, Henriques et al. (1998) tested whether the effect was an effect of eye-position (as in Hill 1972, where the effect appeared to be related to eye-position rather than peripheral viewing), and found that the errors were not a function of eye-position. This again contradicts the findings of Hill (1972) and suggests that effect of gaze position on visual targets is due to errors in localization of stimuli which are viewed (or updated into) the retinal periphery, rather than an effect of misperceiving the angle of gaze on the body.

A large literature has followed up and extended the findings of Henriques et al. (1998). For example, Medendorp and Crawford (2002), showed that visual stimuli located close to the body which are reached for rather than pointed towards are also updated in a gaze-centered reference frame. So it appears that the brain does not only use gaze-centered updating for visual stimuli located far from the body, but also for visual stimuli within peripersonal space. Additional studies have examined the coding of non-visual proprioceptive target locations, and are reviewed in the next section.

Effects of Gaze Direction on Proprioceptive Localization

Behavioral evidence concerning the effects of gaze direction on proprioceptive localization (localization by knowledge of body position) indicates that, curiously, even target locations that were never in view seem to be coded in a gaze-centered reference frame. Blangero et al. (2005) showed that reaches using the right hand to the location of the occluded-from-view (and passively moved) left hand were affected by gaze direction in a manner very similar to that found for visual targets (as in Bock, 1986). Proprioceptive targets also appear to be updated in a gaze-centered reference frame (Fiehler, Rösler, & Henriques, 2010), even when the location is remembered rather than available online (Fiehler, Schütz, & Henriques, 2011; Jones & Henriques, 2010). These effects have been demonstrated not only in sighted individuals, but also in those who have lost vision during their lifetime (Reuschel, Rösler, Henriques, & Fiehler, 2012). However, proprioceptive localization was not affected by gaze direction in the congenitally blind, indicating that the effect is a result of the development of a "visual brain" in early life (Reuschel et al., 2012).

Effects of Gaze Direction on Tactile Perception

Compared to the large literature just reviewed regarding effects of gaze direction on auditory, visual, and proprioceptive locations, there are few studies that have examined the effects of gaze direction on tactile localization. There are however reports of gaze direction affecting reaction times to tactile stimuli (Honoré, Bourdeaud'Hui, & Sparrow, 1989; Lawson, Boylan, & Edwards, 2013; Pierson, Bradshaw, Meyer, & Howard, 1991; Rorden, Greene, Sasine, & Baylis, 2002; Scocchia, Stucchi, & Loomis, 2009). Gazing towards the location of a touch may also modulate event related potentials (ERPs) for tactile stimuli, even when the hand is not actually in view. Forster and Eimer (2005b) found that that when viewing the hand receiving tactile stimulation early ERP components were modulated, probably indicating effects in the Primary Somatosensory Cortex (S1) due to feedback connections from multisensory areas. Gazing in the direction of the hand while the hand is occluded from view modulated later stages of processing. These observations suggest that the tactile sense might also be affected by where one is looking, although improved reaction times and enhanced ERPs, both indicating enhanced sensitivity are generally a consequence of directed attention.

There are some reports of gaze direction affecting some aspects of tactile spatial processing. In a tactile-kinesthetic rod bisection task, holding gaze eccentric caused the middle of the rod to be perceived as shifted in the opposite direction as the gaze direction (Chokron & Imbert, 1993). This indicates an underestimate of the length of the rod on the same side as gaze, or a perceived straight ahead shifted in the opposite direction as gaze.

More recently, Ho and Spence (2007) showed that when gaze was held eccentric, the perceived location of vibrotactile stimuli applied to the torso were perceived as shifted in the direction opposite to the head turn. However, Harrar and Harris (2009, 2010) showed that eye position shifted the perceived location of touches on the forearm in the *same* direction as the direction in which the eyes were turned, regardless of whether the perceived location of the touch was indicated on a visual scale (2009) or by pointing (2010).

Aims of the Present Studies

One of the aims of the current thesis is to confirm and explain the opposite directions of effects found by Ho and Spence (2007) and Harrar and Harris (2009, 2010). In her doctoral thesis, Harrar (2010) proposed that the direction of effect depended on whether the eyes or head were the eccentric effector. When she manipulated eye direction, effects were in the same direction as gaze, whereas when

Ho and Spence manipulated head direction, effects were in the opposite direction as gaze. She speculated that the opposite effects might cancel each other out during normal gaze changes that typically have both eye and head components. However this seems unlikely as the eyes and head tend to move in opposite directions in order to keep the location of gaze constant (the vestibulo-ocular reflex, e.g., Guitton & Volle, 1987). For example, if the head were 15 degrees left of the body and the eyes were 15 degrees right of the head, Harrar's explanation would suggest that touch locations would be shifted further to the right than if only one of the head or eyes were turned, despite that gaze is actually centered in this example.

There were many other differences between the studies conducted by Harrar and Harris, and Ho and Spence: the part of the body stimulated (arm or trunk), the kind of stimulation (solenoid tap or vibration), and the procedure (randomized gaze direction vs. blocked). In Chapter 2 of this thesis I examine whether eye and head position have opposite effects when manipulated concurrently with similar procedures as Harrar used. The results indicate that eye and head orientation in fact have the same effect on tactile spatial localization, both shift perceived locations of solenoid taps to the arms in the same direction as gaze. This therefore cannot be the explanation for the differently directed perceptual shifts observed in the two studies.

In Chapter 3, I begin by successfully replicating the results of Ho and Spence (2007): when the head is held eccentric in a blocked design, vibrations to the torso are perceived as shifted in the opposite direction as gaze. In the next experiment in Chapter 3 I show that if the head angle is chosen randomly and moved for each trial (rather than blocked and not moved) the direction of the effect shifts to be in line with what was found by Harrar and Harris (2009). This allows for a conclusive explanation for why opposite effects were found: it is not due to which effector (eye or head) is eccentric, nor which part of the body is stimulated, nor type of stimulation. The direction of the effect is determined primarily by whether gaze is held eccentric in a blocked design (where no gaze movement is made between trials, or between touch and response), or is randomized between trials (where a movement is made between each trial, and between touch and response), suggesting different frames of reference are used depending on the task.

Next, in Chapter 4, I examine whether there are also effects of gaze direction on touch localization on the back. Since the back of the body cannot normally be viewed, will it also be coded in a gaze-centered frame? Surprisingly, perceived touch locations on the back do exhibit an effect of gaze position, suggesting that they too are coded relative to gaze.

Finally, in Chapter 5, I attempt to determine the underlying cause of the effects of gaze direction on perceived touch location. If the effects are a result of misperceiving the angle of gaze on the body then effects of gaze direction should be a function of gaze angle, with no effect when gaze is centered on the body. In contrast, if the effect is due to misperceiving the location of a touch relative to gaze (similar to the RME described in vision) then effects would depend on the distance between the location of gaze and touch. In addition, I examine whether these effects depend on whether response is made perceptually, by visual comparison or by a method intended to not require crossmodal comparisons, or by action (pointing).

‘

List of Specific Hypotheses in each chapter

Chapter 2:

1. Eye position (relative to head) will have a significant effect on perceived touch location.
2. Head position (relative to body) will have a significant effect on perceived touch location.
3. The effect of eye and head position will be equivalent, and thus the effects will be well described as an effect of gaze (eye + head). Touch localization will be biased in the same direction as gaze.

Previous research has indicated that eye and head orientation affect touch localization in opposite directions (Harrar & Harris, 2009, 2010; Harrar, 2010; Ho & Spence, 2007). However, these studies differed in many aspects in addition to whether eye or head position was manipulated. Therefore, I hypothesize that when all other aspects are held constant, eye and head position will have equivalent effects, as has been found for auditory (Lewald & Ehrenstein, 1998) and visual (Yamaguchi & Kaneko, 2007) localization.

Chapter 3:

1. When gaze position is held eccentric for both tactile target presentation and for localization response, localization will be biased in the direction opposite to gaze.

2. When gaze position is held eccentric for tactile target presentation but returned to a centered position for localization response, localization will be biased in the same direction as gaze.

The studies finding opposite perceptual shifts related to eye (Harrar & Harris, 2009, 2010; Harrar, 2010) and head position (Ho & Spence, 2007) also differed in the dynamics of the tasks involved. Harrar and Harris's experiments involved a randomized order of eye positions and allowed for eye movements before response to foveate the response location. In contrast, Ho and Spence (2007) used a blocked design where head position was oriented to either the left, right, or center for both touch presentation and response. It is hypothesized that it is this critical difference between the studies that explains why opposite effects were found. Findings in support of these hypotheses would indicate that touch localization is coded differently (i.e., in different reference frames) depending on the dynamics of the task.

Chapter 4:

1. When tactile targets are applied to the back of the torso there will be no effect of gaze direction on touch localizations.

This finding would indicate that a gaze-centered reference frame is not used for tactile targets on the back.

Chapter 5:

1. Tactile localization errors will be a function of gaze direction relative to the body, rather than a function of the difference between gaze location and tactile target location.
2. This effect will not depend on whether localization response is made using an action, visual, or numerical representation.

Confirmation of the first hypothesis would indicate that the effect of gaze orientation on target location is due to a misestimate of gaze angle (as proposed by Harrar & Harris, 2009, 2010; Harrar, 2010, and analogous to conclusions of Hill, 1972; McGuire & Sabes, 2009; and Yamaguchi & Kaneko, 2007), rather than due to a misperception of the location of the target relative to gaze (analogous to conclusions of Bock 1989 and Henriques et al. 1998).

Confirmation of the second hypothesis would confirm findings from Harrar and colleagues who concluded that gaze direction affects tactile localization in the same manner whether response is made by a visual comparison (Harrar & Harris, 2009), pointing (Harrar & Harris, 2010), or a numerical representation of location (Harrar, Pritchett, & Harris, 2013). However, each of these studies was conducted with different participants so direct comparisons between studies could not be conducted. Therefore, in chapter 5 I use three response methods (with order counterbalanced) for the same set of participants so that direct comparisons can be made.

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Chapter 2: Perceived Touch Location is Coded Using a Gaze Signal

Abstract

The location of a touch to the skin, first coded in body coordinates, may be transformed into retinotopic coordinates to facilitate visual-tactile integration. In order for the touch location to be transformed into a retinotopic reference frame, the location of the eyes and head must be taken into account. Previous studies have found eye position related errors (Harrar & Harris, 2009) and head position–related errors (Ho & Spence, 2007) in tactile localization, indicating that imperfect versions of eye and head signals may be used in the body-to-visual coordinate transformation. Here, we investigated the combined effects of head and eye position on the perceived location of a mechanical touch to the arm. Subjects reported the perceived position of a touch that was presented while their head was positioned to the left, right, or center of the body and their eyes were positioned to the left, right, or center in their orbits. The perceived location of a touch shifted in the direction of both head and the eyes by approximately the same amount. We interpret these shifts as being consistent with touch location being coded in a visual reference frame with a gaze signal used to compute the transformation.

Introduction

A challenge in understanding multisensory integration is how the human brain integrates spatial information from different modalities all coded in different reference frames. One theory is that there is a multimodal map that integrates multisensory information into a single spatial representation. To transform between body coordinates and retinotopic coordinates, the brain must consider the current posture of the body as well as either (1) the location of the eyes and the head or (2) the location of gaze (because gaze is the sum of eye and head positions). If tactile information were coded in retinotopic coordinates, then any errors in the representation of the position of either the eye or head would cause systematic shifts in touch localization.

Errors in coding the position of the eyes (Harris & Smith, 2008) and systematic shifts in tactile localization related to eye and head positions have previously been demonstrated (Harrar & Harris, 2009, 2010; Ho & Spence, 2007), suggesting that touch is indeed coded in retinotopic coordinates. Eye position was found to cause shifts in the location of touch in the same direction as eye position (Harrar & Harris, 2009), while head position has been found to cause shifts in the opposite direction (Ho & Spence, 2007). This would suggest that eye and head positions are coded separately in the sensory transformation, with the signal for eye eccentricity being underestimated and the signal for head eccentricity being overestimated. Large differences between the techniques using head and eye positions in these studies make comparing their results difficult. The research on eye position used solenoid touches on the arm while the head position research used vibration on the torso. The two studies also had substantial procedural differences. The present study allows for comparison of the effects of head and eye eccentricity on touch localization directly.

Errors due to eye and head positions have been found for auditory (Collins, Heed, & Röder, 2010; Goossens & Van Opstal, 1999; Graziano, 2001; Kopinska & Harris, 2003; Lewald & Ehrenstein, 1996a, 1996b, 1998; Lewald, 1998) visual (Harris & Smith, 2008; Kopinska & Harris, 2003; Wexler, 2003), and proprioceptive (Fiehler, Rösler, & Henriques, 2010; Lewald & Ehrenstein, 2000) localization, suggesting that spatial information across all these senses may be integrated into a single common retinotopic reference frame.

The majority of this research has investigated either the effect of eye position or the effect of head position on spatial localization but, to our knowledge, only one study has directly compared the effects of eye and head positions and how they combine. Lewald and Ehrenstein (1998) reported that both head and eye position affected the perceived location of a sound and that both effects were in the same direction (opposite to the direction of the head and eye) and of approximately the same magnitude. When the eyes and head were in opposite directions (e.g., eyes 30 degrees left and head 30 degrees right, such that gaze remained straight ahead), the effects appeared to cancel out indicating linearly combining effects.

We investigated the effects of eye and head position on the perceived location of touch. Participants held their head to the left, right, or center of their body and their eyes to the left, right, or center in their head while a touch was applied to the arm. Participants reported the position of the touch relative to a visual probe. They centered their eyes and heads before the probe was presented in order to avoid any possible effects of eye and head positions on the perceived location of the probe.

Methods

Participants

Four women and six men with an average age of 32 years participated. One male participant was left handed, and all others were right handed. All had normal or corrected-to-normal vision. Experiments were approved by the York Ethics board.

Apparatus

The touch apparatus consisted of two solenoids encased in a box with pins facing upwards. When power (amplified 5 volt signals from a CED1401 interface box (Cambridge Electronic Design, Cambridge, UK) controlled by a PC) was delivered to each solenoid its pin extended about 2 mm from the surface of the box for 50 ms. The pins were located at approximately 6 and 11.5 cm from the subject's wrist (or 2.5 degrees left and 3.5 degrees right of straight ahead) (see Figure 2.1).

A flat screen computer monitor (54 cm, resolution 1600 x 1200 pixels) was positioned vertically 5.2 cm behind the solenoids and 29 cm from the viewer. It was used to display gaze and head fixation points as well as a probe line used for comparison with the perceived location of the touch. The probe line was a 15 cm long, one pixel wide, red, vertical line positioned on the screen with its top 5.5 cm (10.7 degrees) below the gaze fixation points. The bottom of the probe line was at the bottom of the screen, which was at the same height as the arm when positioned over the solenoids.

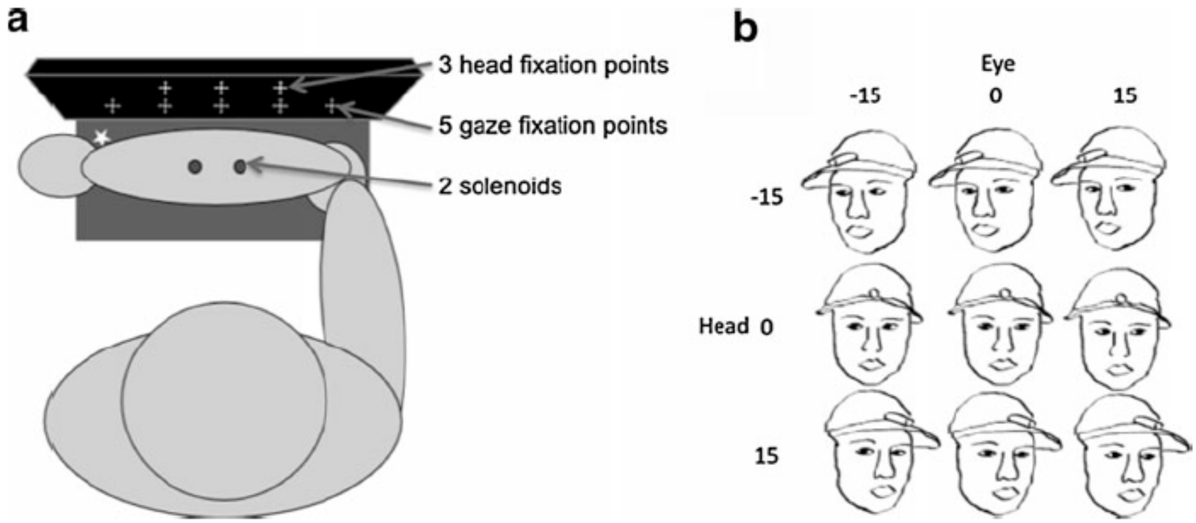

Figure 2.1. Apparatus set up and experimental conditions. A: Touch locations were at 6 degrees left and 7 degrees right from straight ahead, or 6 and 11.5 cm from a star on the box that encased the solenoids. The star was approximately aligned with the wrist crease. The screen displaying fixation points and a probe line was positioned directly behind the touch box, 5.2 cm behind the solenoids and 29 cm from the viewer. The bottom edge of the screen was level with the top of the solenoids. B: For each of three head positions (15 degrees to the left, 15 degrees to the right, and centered), three eye positions were used, such that the eyes could be centered or at 15 degrees to the left or right in their orbits. Nine combinations of eye and head positions led to five different gaze positions, 30 degrees to the left and right, 15 degrees to the left and right, and centered. A laser mounted to the head allowed for precise control of head position.

Controlling Head and Eye Position

Participants wore a baseball hat with a laser pointer attached to the rim. They aligned the laser beam with head fixation targets presented on the screen. Three head fixation points were used: -15° (left), 0° (straight ahead) and +15° (right). For each head fixation, three eye fixations were used: -15° (left in head), 0° (centered in head) and +15° (right in head). Thus, five gaze fixation points were needed (-30, -15, 0, +15, +30°, relative to the body straight ahead). Head fixation points were positioned at the approximate height of the laser point projected from the hat and gaze fixations were positioned 3 cm below the head fixations at eye height. Figure 2.1 shows the arrangement of the apparatus and the head and gaze fixation points.

Procedure

Participants were seated in front of the apparatus and wore headphones to muffle the sound of the touches and a baseball hat with mounted laser pointer. The hat was adjusted such that the laser pointed directly at the "centered" head fixation point when their head was oriented straight ahead. Participants then positioned their arm across the touch box and aligned their wrist crease with a star on the box (see Figure 2.1).[1]

Each trial began with head and eyes centered. A head fixation cross was displayed in one of the 5 locations, and the participant was allowed 1 s to turn their head and point the head-mounted laser at the cross. Next, a gaze fixation point was displayed that the participant foveated. One second later, both the gaze and the head fixation points were removed from the screen. The subject maintained their head and eye position while a touch was administered at one of the two locations on the arm. A central fixation point was presented 500ms after the touch for duration of 2 s, directing participants to recenter their head and eyes before responding. After the

[1] Exact lining up of the arm on the stimulation box was not necessary as judgments were made between the location of the solenoids and the reference line on the screen which were fixed relative to each other.

head and eyes were recentered, a vertical line probe was presented. Subjects were allowed to move their eyes to the line to make a judgment regarding whether the line was to the left or right of where they were touched. The line remained visible until a response was made, using left and right foot presses. The subject's response initiated the next trial.

The position of the line probe was controlled by a best PEST adaptive procedure (Pentland, 1980). For the first trial of each condition, the location of the reference line on the screen was chosen randomly. In subsequent trials, the reference line was moved to the left or right depending on the participant's response to the previous occurrence of that condition. Step size was initially 100 mm and was halved after each reversal and doubled after three consecutive steps in the same direction. The minimum step size was 1 mm. Once the minimum step size was reached, the PEST staircase terminated for that condition and the final location of the probe line was taken as the perceived touch location. Staircases for each of the 18 conditions were interleaved and randomly selected during testing. The entire session lasted approximately 50 min.

Results

Figure 2.2 plots the effect of gaze on perceived touch location. A three-way repeated measures ANOVA was conducted for effects of touch location, eye eccentricity, and head eccentricity. Eye position significantly affected perceived touch location (F (2,18) = 4.37, p = .033, η^2_P =.33). When the eyes were to the left in their orbits, the perceived location of the touch appeared displaced to the left, and when eyes were to the right in their orbits, the perceived location of the touch was displaced to the right relative to the perceived location when the eyes were straight ahead. Similarly, perceived touch location was significantly influenced by head position. The perceived location of the touch was displaced in the same direction as the head (F (2,18) = 6.03, p = .01, η^2_P =.40). A significant effect of solenoid location (F (1,9) = 79.08, P < .001, η^2_P = .90) confirmed that perceived touch location was related to the area of skin where the touch was administered and that the two touches could be discriminated. No significant interactions were found, indicating that the effects of eye and head position were independent (F (4, 36) = 0.82, p = .52). Also, the effect of eye (F (2, 18) = 2.70, p = .09) and head (F (2, 18) = 0.14, p = .87) position did not depend on touch location. The three-way interaction was also not significant (F (4,36) = 1.04, p = .40).

A direct comparison of the effects of eye and head positions is presented in Fig 2.3, which plots the effects of eye position (collapsed across head position) and the effects of head position (collapsed across eye position) superimposed on each other. The regression lines presented in Figure 2.3 show an average effect of +0.30 mm of touch displacement per degree of eye eccentricity and +0.48 mm touch displacement per degree of head eccentricity. If the effects of eye and head positions differ, an interaction of body part and direction of eccentricity should be found. A three-way repeated measure ANOVA was conducted with body part (eye or head), direction of eccentricity (15° left, center, or 15° right), and touch location as factors. The body part by direction of eccentricity interaction was not significant (F (2,15) = 0.17, p = .80). Similarly, no significant effect of body part (head or eye) was found (F

(1,9) = 0.13, p = .73). Together, these results indicate that the head and eye effects were not significantly different.

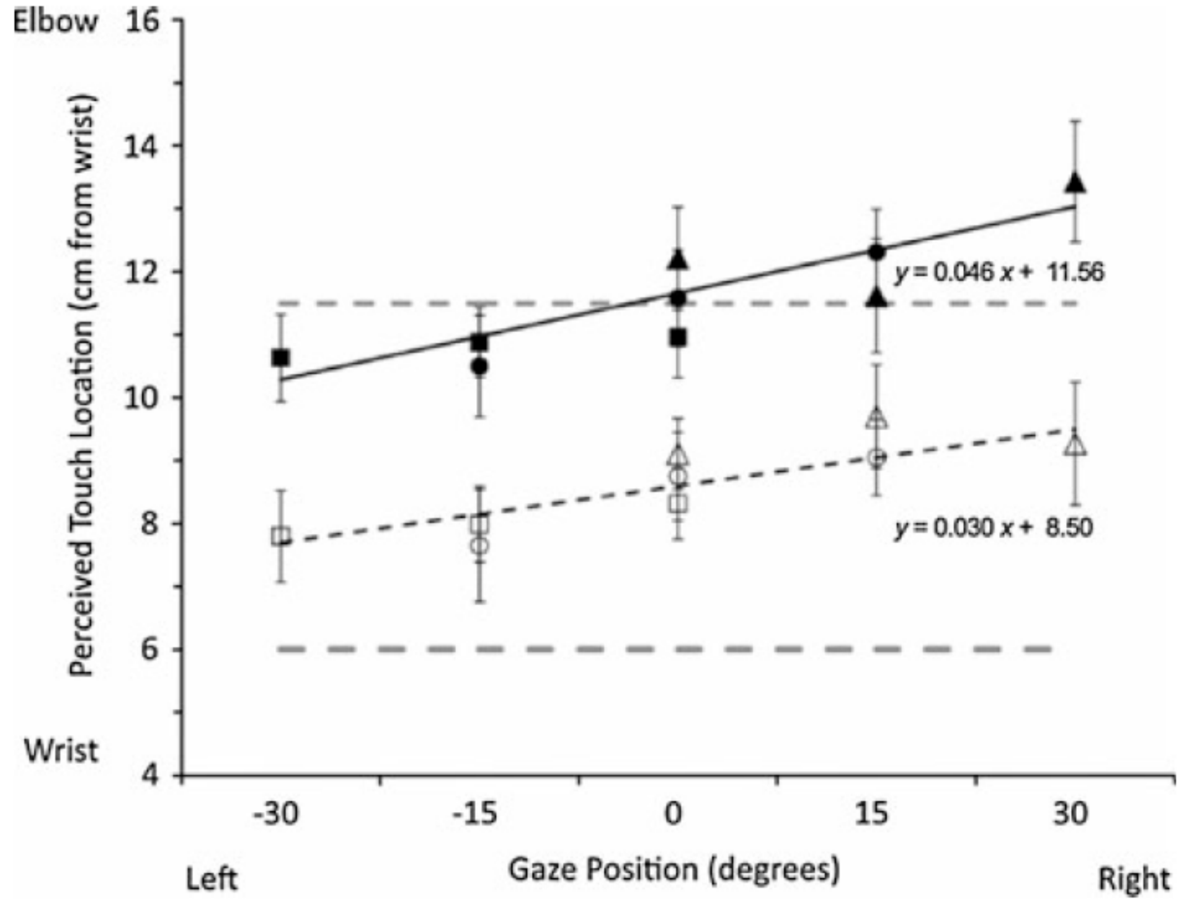

Figure 2.2. Effect of gaze position on perceived touch location on the right arm. Data points represent the results for each solenoid for each combination of head and eye position. Data for the eye positions at a particular head position are marked by different symbols (square for head 15 degrees left, circle for head centered, and triangle for head 15 degrees right). Error bars show one standard error of the mean. Regression lines are fitted to the entire data set for each solenoid. The regression equations are indicated on the figure. Dashed gray lines indicate the actual location of each solenoid. Larger numbers for gaze position and perceived touch location indicate positions further to the right and toward the elbow. Gaze shifted the perceived location of touches by 0.38 mm per degree of eccentricity.

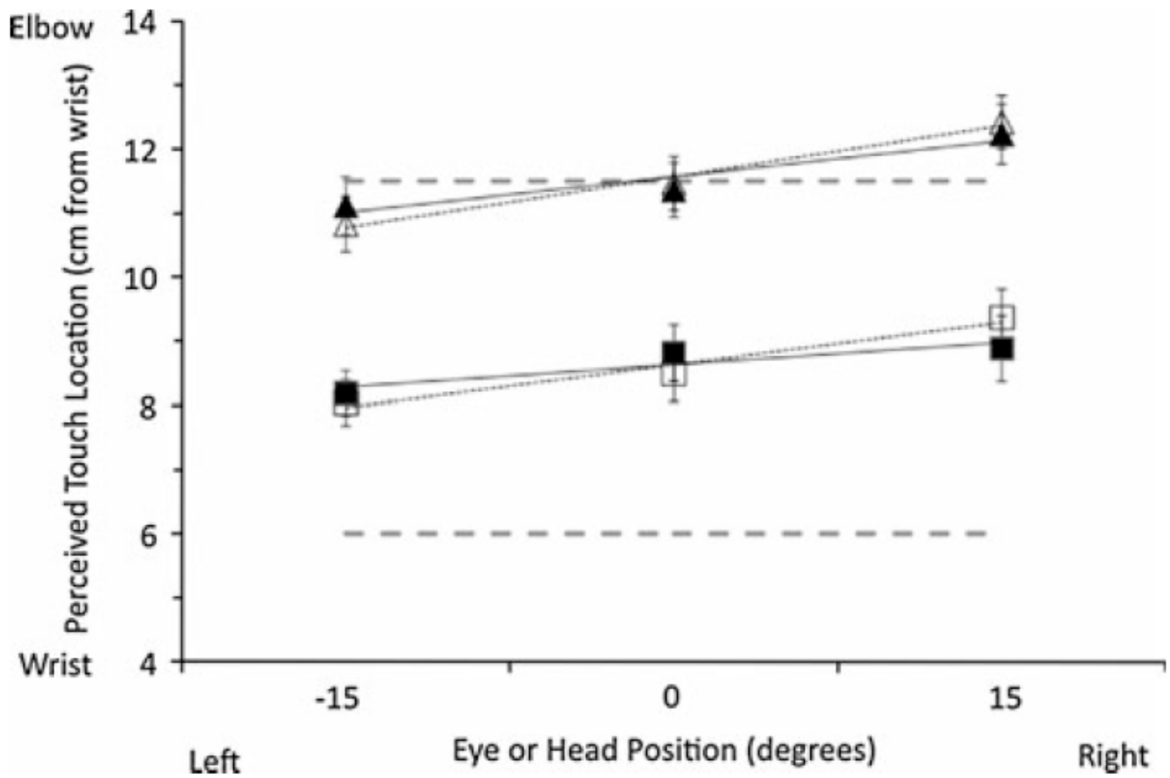

Figure 2.3. The effects of eye-in-head (filled symbols) and head-on-body (open symbols) on perceived touch location for the two touch locations (squares and triangles) were similar. Data for eye position were obtained by averaging across head position. Data for head position were obtained by averaging across eye positions. Error bars show one standard error of the mean. Regression lines were fit to the data points shown for the average effect of head and eye position for each solenoid. The effect of eye position was 0.37 and 0.23 mm per degree of eccentricity for solenoids at 11.5 and 6 cm from the wrist, respectively. The effect of head position was 0.53 and 0.44 mm per degree of eccentricity for the same two solenoids. Larger numbers for eye or head position and perceived touch location indicate positions further to the right and toward the elbow.

Discussion

The perceived location of a mechanical touch on the arm was found to shift in the same direction as an eccentric eye or head position and by approximately the same amount in each case. The effects were independent of one another and appeared to be linear over the +/-15-degree range tested. This is consistent with a gaze signal being used to convert between body and retinotopic coordinates. If a different reference frame were used, gaze position would not be necessary to compute the transform and gaze-related errors would not be expected. This conversion may be done in order to represent tactile and visual locations in the same coordinates.

Our findings add to converging evidence that touch location is coded in an egocentric visual reference frame. Research using transcranial magnetic stimulation indicates that the posterior parietal cortex remaps touch location from body to external or visual coordinates (Azañón, Longo, Soto-Faraco, & Haggard, 2010; Bolognini & Maravita, 2007). Also, blind people appear to code touch location differently from sighted individuals (Röder, Föcker, Hötting, & Spence, 2008; Röder, Rösler, & Spence, 2004), supporting the idea that a visual coordinate system is normally used in tactile coding.

Shift of Perceived Touch Location with Head Eccentricity

The perceived location of sounds and lights have been found to depend on head position but only one previous study has looked at the effect of head position on the perceived location of tactile stimuli. The head position related shift we report here is at odds with the results of that study. Ho and Spence (2007) found that the perceived location of a touch indeed shifted related to head position, but in the direction opposite to head position. The magnitude of the shift we report is also larger than Ho and Spence observed. The head-related shifts noted in the present study were of the order of +0.48 mm per degree of head eccentricity, whereas data from Ho and Spence yield an effect size of only -0.05 mm per degree.[2]

The difference in the magnitude of effects between the two studies may be partially due to different head displacements. Our head position range was only +/-15 degrees, while Ho and Spence (2007) used head positions of +/-90 degrees. If head position had larger effects near center but the effect saturated at large head positions, this could lead to the much smaller effect size reported by Ho and Spence. Such a saturation of effects may result because of the physiology of head movements, where only about 50% of the total range of rotation actually result from the head rotating around the top two vertebrae, while the additional 50% of rotation of the head comes from rotations within the spine itself (Fielding, 1964). If the signal for head displacement from the head rotation around the spine were subject to systematic errors but the signal related to the rotation of the spine was not, the effect would be expected to asymptote at that rotation.

The pattern of stimulation used is another factor that might contribute to the differences in magnitude in the two studies. Ho and Spence (2007) used vibrotactile stimulation at 250 Hz while we used a 50 ms mechanical depression of the skin. These different types of stimulation are encoded by different touch receptors. Our stimulus would optimally stimulate the slowly adapting Merkel receptors, which are the smallest and most useful receptors for tactile spatial localization. In contrast, the

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[2] Ho and Spence (2007) reported data as numbers between 0 and 1 representing the proportion of distance along a tactor-mounted belt. To calculate the perceived location of touches in cm, we multiplied the numbers reported by 28 cm, the distance between the tactors. Head positions used in the calculation were as reported, +/-90 degrees as well as straight ahead.

vibrotactile stimulation at 250 Hz used by Ho and Spence would optimally stimulate the very rapidly adapting Pacinian corpuscle receptors, which are most sensitive to vibration and have large diffuse receptive fields. The pathways from these receptors are anatomically distinct from the slowly adapting touch receptor system (Friedman, Chen, & Roe, 2004) and may correspond to different cortical maps. Vibration-based maps are likely to be less precise which might explain the smaller effect sizes reported by Ho and Spence (2007).

Another possible explanation for the difference in magnitude might arise from the fact that Ho and Spence (2007) used blocked trials at each head position. Since the head remained at an extreme position for several minutes, adaptation could have occurred causing a shift of perceived straight-ahead toward the current head position. As little as 3 min of eccentric head position has been shown to cause a 10% adaptation in perceived straight ahead (Lackner, 1973). This might cause a drastic reduction in the systematic errors caused by the head position signal, possibly even reversing them.

Finally, the body part where touches were administered could contribute to the different pattern of errors found. We applied touches to the skin of the forearm, whereas Ho and Spence (2007) used touches on the torso. It is possible that touches to the arm and the torso are coded in different ways, causing different patterns of errors. Perhaps the visual representation of the torso is left–right reversed (as we are more used to seeing our own torsos in a mirror).

Clearly, more thorough investigation into the effects of eye and head positions on touches stimulating different parts of the body and different receptor types is warranted.

Shift of Perceived Touch Position with Eye Eccentricity

The eye position related shift we report here confirms the findings of Harrar and Harris (2009) that eye eccentricity shifts mechanical touches on the arm in the same direction as eye position. The present study showed that eye eccentricity shifted the perceived location of touches by +0.38 mm per degree whereas Harrar and Harris report a figure of +0.68 mm per degree. While both studies used the same single mechanical touch to the same part of the arm with interleaved eye position conditions, there are some differences between the two studies. Harrar and Harris touched the left arm while here the right arm was touched. Differing magnitudes of effect could reflect an asymmetry related to arm dominance; perhaps the right arm has touch coded more accurately compared to the left. Also, the method of response was different. In the study by Harrar and Harris (2009), participants respond by reading the location of perceived touch off a ruler placed adjacent to the touch box. The eyes scanned the ruler and were not returned to a central position during the reporting. It is therefore possible that there were effects of eye position on the perceived position of the probe (ruler) as well as on the touch, thus magnifying the apparent effect. In the present study, the eyes were returned to center before responding and the more psycho- physically robust PEST method was used.

Shift of Perceived Touch Position with Attention

An alternative explanation for our results is that perceived touch position is shifting with attention, rather than specifically due to eccentricity of the eyes and head. This hypothesis was tested by Harrar and Harris (2009). They had participants maintain a centered eye and head positions while an LED flashed eccentrically diverting participant's attention in that direction. Participants received a touch on their arm while their attention was diverted and then indicated the location of the touch. The perceived location of the touch was found to shift in the direction of attention but accounted for only about 17% of the effect of eye position. We expect that attention played a similar role in the present experiment and contributes only a small amount to the magnitude of shift we report.

Localization Accuracy

While the perceived position of the touch closer to the elbow was accurate when fixating straight ahead, the touch closer to the wrist was always shifted toward the elbow as can be seen in Figures 2 and 3. The pattern of touch being perceived as closer to the elbow is consistent with other findings that touches on the forearm are perceived proximally to their actual location (Cody, Garside, Lloyd, & Poliakoff, 2008).

Are Conversions to Head and Retinal Coordinates done in Series or Parallel?

The systematic errors in perceived location of touch due to eccentric eye and head positions reflect systematic underestimations that are made when accounting for eye and head positions during the reference frame conversion. How these conversions are accomplished is not well understood. It could be that the eye and head positions are accounted for separately, both causing small, independent effects on perceived touch location, reflecting a sequential conversion from body to head to retinal coordinates. Alternatively, eye and head positions could be combined into a gaze signal at an earlier stage of processing, so that only the position of gaze is needed to convert touch location into a visual reference frame. The superior colliculus codes desired gaze in a single signal, with contributions of head and eye position accounted for downstream (Freedman & Sparks, 1997; Klier, Wang, & Crawford, 2001). Our data suggest that the neural code used in tactile-to-visual coordinate transformations uses a single gaze signal of that type, rather than individual signals for eye and head positions.

Conclusion

Gaze eccentricity caused a shift in perceived tactile localization. The effect was the same whether it was due to eye or head displacement. This supports of the idea that touch location is transformed into retinotopic coordinates and that a gaze signal is used to compute the transformation.

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Chapter 3. Reference Frames for Coding Touch Location Depend on the Task

Abstract

The position of gaze (eye plus head position) relative to body is known to alter the perceived locations of sensory targets. This effect suggests that perceptual space is at least partially coded in a gaze-centered reference frame. However, the direction of the effects reported has not been consistent. Here, we investigate the cause of a discrepancy between reported directions of shift in tactile localization related to head position. We demonstrate that head eccentricity can cause errors in touch localization in either the same or opposite direction as the head is turned depending on the procedure used. When head position is held eccentric during both the presentation of a touch and the response, there is a shift in the direction opposite to the head. When the head is returned to center before reporting, the shift is in the same direction as head eccentricity. We rule out a number of possible explanations for the difference and conclude that when the head is moved between a touch and response the touch is coded in a predominantly gaze-centered reference frame, whereas when the head remains stationary a predominantly body-centered reference frame is used. The mechanism underlying these displacements in perceived location is proposed to involve an underestimated gaze signal. We propose a model demonstrating how this single neural error could cause localization errors in either direction depending on whether the gaze or body

midline is used as a reference. This model may be useful in explaining gaze-related localization errors in other modalities.

Introduction

The multiple sensory modalities contribute spatial information each in a unique reference frame. Visual stimuli are initially coded in retinal coordinates, tactile stimuli relative to the skin surface, and auditory stimuli relative to the head. These initial representations of stimulus location are constrained by the anatomy of the sensory receptors and they need to be converted into other reference frames to provide perceptually useful information, such as location in space. Higher levels of processing combine information arising from different sensory modalities into a single coordinate system or else some hybrid system of multiple simultaneous reference frames (Andersen, Snyder, Li, & Stricanne, 1993; Cohen & Andersen, 2002; Colby, 1998; Deneve & Pouget, 2004). Previous studies have suggested that a gaze-based reference frame may be the most likely candidate (Azañón, Longo, Soto-Faraco, & Haggard, 2010; Bolognini & Maravita, 2007; Harrar & Harris, 2009, 2010; Knudsen & Knudsen, 1985; Röder, Föcker, Hötting, & Spence, 2008; Röder, Rösler, & Spence, 2004).

If stimuli are coded relative to gaze, then a gaze signal is required to transform the location from the reference frame of the end organs to the central representation. Any systematic errors in coding the position of gaze would, therefore, shift the perceived location of stimuli. Indeed, several authors have demonstrated that eye position is underestimated (Harris & Smith, 2008; Hill, 1972;

Morgan, 1978) and corresponding systematic errors in localizing various stimuli have been reported related to eye position (auditory: Lewald & Ehrenstein, 1996a, 1996b; Weerts & Thurlow, 1971; visual: Bock, 1986; Fiehler, Rösler, & Henriques, 2010; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Lewald, 1998; tactile: Harrar & Harris, 2009, 2010). Similarly, eccentric head orientation has also been found to produce errors in localizing auditory (Goossens & Van Opstal, 1999; Lewald, Dörrscheidt, & Ehrenstein, 2000; Lewald & Ehrenstein, 1998), visual (Kopinska & Harris, 2003; Wexler, 2003), and tactile stimuli (Ho & Spence, 2007; Pritchett & Harris, 2011).

The effects of eye and head position on tactile (Pritchett & Harris, 2011) and auditory (Lewald & Ehrenstein, 1998) localization are equivalent. This equivalency suggests that head and eye position may be combined into an encompassing gaze signal that then forms the reference for spatial locations. This is consistent with research showing that several monkey cortical and subcortical areas use a single signal for gaze where eye and head information is combined (Martinez-Trujillo, Klier, Wang, & Crawford, 2003).

Although it is known that stimuli are systematically mislocalized when gaze is eccentric, there are inconsistent reports on the nature and direction of these localization errors. In auditory perception, most reports are of perceived locations shifting opposite to eccentric eye or head position (Goossens & Van Opstal, 1999; Lewald et al., 2000; Lewald & Ehrenstein, 1996b, 1998; Lewald, 1998) although there are some reports of the perceived location of auditory targets shifting in the same direction as gaze (Lewald & Ehrenstein, 1996a; Weerts & Thurlow, 1971).

Most pertinent to the current study are the contrasting directions of tactile mislocalization found in response to head position. Ho and Spence (2007) reported that, when participants localized vibrotactile stimuli presented on the waist while holding an eccentric head orientation, tactile localization was biased in the direction opposite to head position. In contrast, results from this laboratory have demonstrated that brief touches presented on the forearm were mislocalized in the same direction as eye (Harrar & Harris, 2009, 2010) and head position (Pritchett & Harris, 2011). The current study was therefore conducted to resolve this discrepancy

Comparing the studies on tactile localization errors related to head position (Ho & Spence, 2007 vs. Pritchett & Harris, 2011) is not straightforward as the studies differ along important dimensions. First, different types of touch stimuli were used and thus different sensory pathways could potentially lead to differences in the subsequent position coding. Ho and Spence (2007) used vibrotactile stimuli at 250 Hz which are primarily detected by the deep layer Pacinian corpuscles that have large receptive fields (Jänig, Schmidt, & Zimmermann, 1968). Pritchett and Harris (2011) used brief discrete solenoid touches that are detected primarily by surface layer Merkel receptors with receptive fields substantially smaller than Pacinian corpuscles (Johansson & Vallbo, 1979). There is evidence that information from these different receptor types may be coded in different cortical maps (Friedman, Chen, & Roe, 2004) that may underlie the different results reported using these different tactile stimuli. Second, Ho and Spence (2007) tested tactile localization on the front of the waist while Pritchett and Harris (2011) tested the forearm. These two body parts utilize different body landmarks as tactile reference frames, which may lead to unique localization biases (Cholewiak, Brill, & Schwab, 2004 for abdomen, Cholewiak & Collins, 2003 for forearm). Finally, in addition to type and place of stimulation, the studies used different experimental procedures. Different task demands could lead to different location-encoding mechanisms. In the study by Ho and Spence (2007) participants both received stimuli and made their responses while their heads were eccentrically positioned, while Pritchett and Harris (2011) had participants return to straight ahead before responding.

We first replicated and extended the Ho and Spence (2007) studies using the same kind of stimulation (250 Hz vibration) and body part (torso) with the participants both receiving stimuli and making responses with an eccentric head position. In Experiment 2, we used the same stimuli and body part but a protocol similar to that of Pritchett and Harris (2011) where participants received tactile stimuli in an eccentric head position but returned to center before responding. Results indicated that it was the type of task that determined the direction of localization errors and ruled out the other possible factors listed above.

Experiment 1 and 2 Method

Participants

Eight participants (4 male, 4 female, mean age 28 years) volunteered to participate in Experiment 1. Experiment 2 had eight participants (4 male, 4 female, mean age 31 years), six of whom also participated in Experiment 1. All reported having a normal sense of touch and normal or corrected-to-normal vision. All experiments were approved by the ethics board of York University and followed the guidelines of Helsinki.

Apparatus

The vibrotactile stimuli were presented using an array of eight tactors (Model C2, Engineering Acoustics, Florida, USA) for all experiments. The tactors were mounted on a belt worn around the participant's waist. The eight-tactor array was centered on the participant's belly button with the center of each tactor 4 cm from the next. The vibrotactile stimuli were at 250 Hz and were of 50 ms duration. The intensity of each touch was randomly chosen from four possibilities (37.5, 50, 62.5, or 75% of maximum intensity) in order to keep participants from distinguishing the tactor locations by learning any subtle differences in their intensities.

Head and eye position were manipulated by fixation points positioned in space and a laser mounted on a hat worn on the participant's head. During testing participants were seated in a darkened room in a chair chosen for its high supportive back extending above the head. Participants maintained a seated upright posture in all experiments. Each experiment used a slightly different setup of chair position and fixation points to facilitate the different experimental procedures (see Figure 3.1). The details specific to each procedure are described below.

A 21-inch LCD computer monitor was used to display a visual scale (described below) for recording the perceived location of touches and to display fixation points. For all experiments, the computer monitor was 55 cm from the

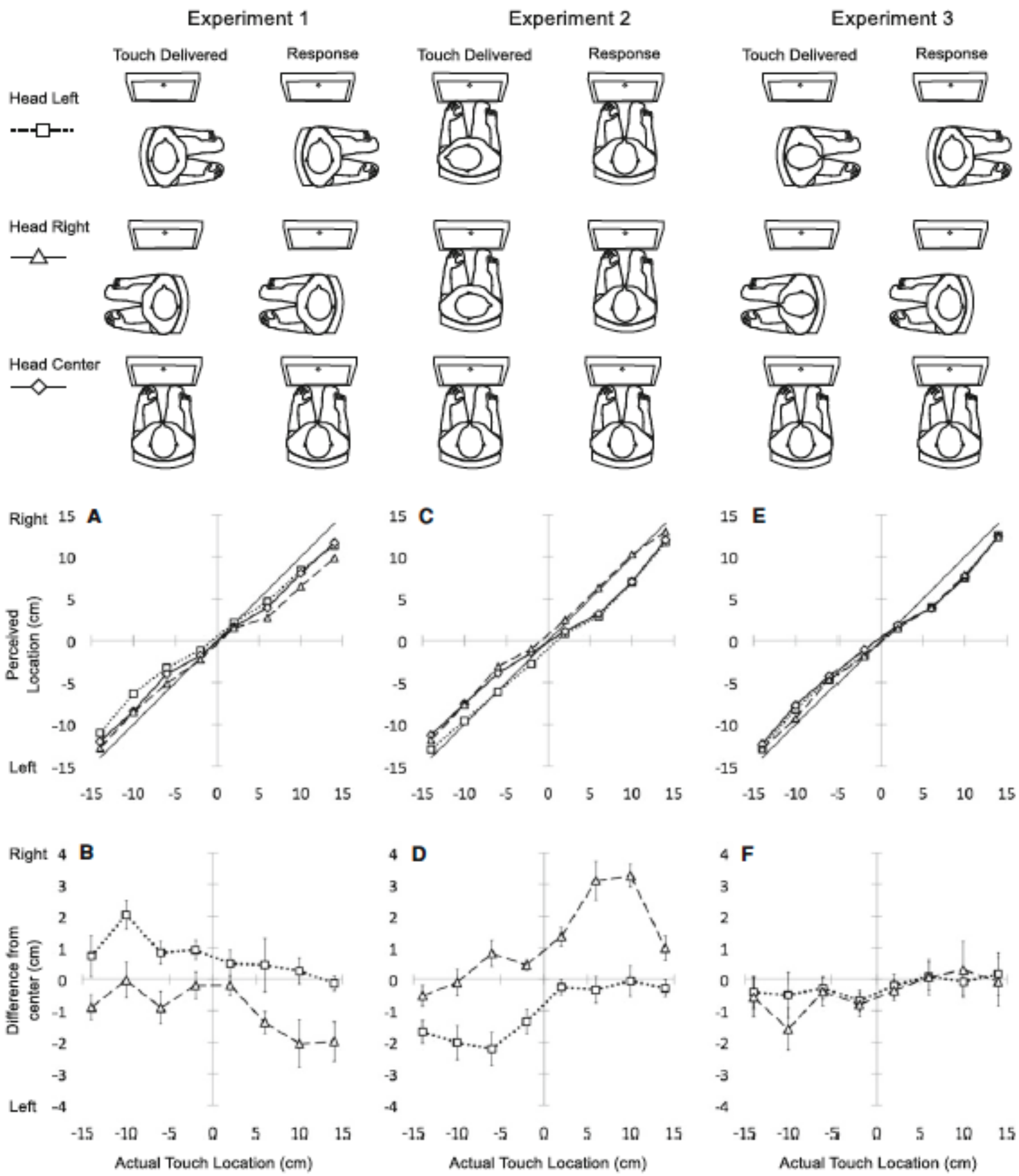

Figure 3.1. Head and body positions during touch delivery and response are illustrated for each experiment. In Experiment 1, head position was manipulated in a blocked design as in Ho and Spence 2007: the head was eccentric for touch delivery and during reporting perceived touch location. In Experiment 2, head position was manipulated in a randomized design, and the head was always returned to the center to report touch location. In Experiment 3, the touch was always delivered with head centered and the head then turned before responding. In A, C and E perceived locations (related to the body midline at 0) of the 8 tactors under head left (dotted line, square symbol), head right (dashed line, triangle symbol) and head center (solid line, diamond symbol) are shown for each of three experiments. Standard error bars are the size of the symbols. In B, D and F the difference between the head-eccentric and head-centered locations are illustrated for the three experiments. Error bars show one standard error of the mean.

viewer when the visual scale was presented. Participants used a cordless optical mouse to indicate the perceived location of the touch on the scale.

Visual Scale for Reporting Perceived Touch Location

Before beginning each experiment, the vibrotactile stimuli were delivered from each tactor in order from the furthest right to the furthest left. Participants were instructed to memorize the location of the endpoints of the array and to use the endpoints of a white bar (35.3° x 0.62° visual angle) presented on the screen to represent those locations (as in Ho and Spence 2007). Participants reported the perceived location of touches by moving a sliding bar (0.51° x 0.77° visual angle) along the scale by means of a mouse. The bar could be moved by dragging it, by clicking on the desired location on the scale, or by clicking the left or right spaces at the end of the scale. When the participant was happy with the positioning of the vertical bar they clicked on an ‘‘OK’’ button at the bottom of the screen. This response method is the same as used by Ho and Spence (2007). The unique details for each experiment are described below.

Experiment 1

The first experiment was a replication of Ho and Spence (2007). One change from their protocol was the use of the head laser to enable participants to reliably position their heads in all conditions. Participants were arranged with their head either 90° left, 90° right or straight with the screen straight ahead of them (Figure

3.1). Each trial began with a fixation cross displayed centered on the screen, the head-mounted laser was illuminated and the participant fine adjusted their own head position. This was done to make the conditions as similar as possible between all the experiments. After 2 seconds the fixation cross and laser were turned off and a vibrotactile stimulus was presented from a randomly chosen tactor along the array. The visual scale was displayed on the screen 500 ms later and the participant indicated the perceived location of the touch. Clicking the ‘‘OK’’ button led to the beginning of the next trial. Each of the eight tactors was presented 12 times which took about 7 min. Once the block was complete, the experimenter moved the chair into the next position (see Figure 3.1) and the next block of trials commenced until all three head conditions had been run. Running order was counterbalanced across participants.

Experiment 2

The second experiment followed a procedure similar to Pritchett and Harris (2011) but with the vibrotactile stimulation on the torso and the response measure (the visual scale) that was used by Ho and Spence (2007). The chair was positioned so that the participant looked at the computer monitor with their head and eyes straight ahead. Target LEDs to indicate required eye and head position were positioned 90° to the left and 90° to the right of the participant.

Each trial began by directing the participant to the fixation position for that trial. If it was a head-centered trial, the fixation cross on the screen was presented. If it was a left or right head condition trial, an arrow was displayed on the screen pointing in the appropriate direction, left or right. The participant was given 2 seconds to turn their head to the specified direction and to align their head-mounted laser to the illuminated LED at 90°. After 2 seconds the fixation point was removed, the head laser turned off, and the vibrotactile stimuli were presented from a randomly chosen location on the tactor array. The head laser then turned on again and the participant turned their head back to align the laser with a centered fixation point before reporting the location of the touch on the visual scale. The next trial began when they clicked the "OK" button. Each of the eight tactors was presented 12 times for each head condition for a total of 288 trials. The experiment was approximately 21 minutes in duration.

Data Analysis

Participants reported the perceived location of touches on a linear scale. The furthest left end was coded as 0, and the furthest right end was coded as 1. Data were transformed into cm from navel by multiplying by 28 cm, the distance between the first and last tactor and subtracting 14. For each participant the mean reported position for each touch location at each head position was averaged over 12 trials. This perceived location data were subjected to a two-way repeated-measures ANOVA. The effect of head position was quantified by calculating the difference between the perceived location of a touch during the eccentric head condition and the perceived position of the same touch during the centered head condition. This absolute difference from center data was used as an index of the magnitude of the effect of head position. It was also subjected to a two-way repeated-measures ANOVA for each of the three experiments.

Experiment 1 and 2 Results

Experiment 1

The mean perceived location of touch with the head held eccentric is plotted in Figure 3.1a. A significant effect of touch location (F (7, 49) = 248.67, p < 0.001) confirmed that the touch locations could be discriminated. A main effect of head position was also found (F (2, 14) = 15.92, p < 0.001) indicating that the perceived position of a touch was influenced by head position. A trend analysis indicated that the effect of head position was linear (F (1, 7) = 25.06, p = 0.002), meaning that left and right head position affected touch location similarly in magnitude but in opposite directions. Touches were perceived furthest to the left in the right head condition (M = 1.03 cm left), more medially in the centered head condition (M = 0.12 cm left), and furthest to the right in the left head condition (M = 0.60 cm right). There was not a significant interaction of head position and touch location (F (14, 98) = 1.45, p = 0.147).

Further analysis of the effect of head position was conducted using the difference between the perceived position of each touch during the head-eccentric trials (left or right) and the perceived position of the same touch during the head-centered trials (Figure 3.1b). The average unsigned difference between eccentric and centered head position was used as an index of the magnitude of the effect of head position. These data were subjected to a two-way repeated-measures ANOVA.

The main effect of head position was not significant (F < 1, ns), indicating that left and right head position effect touch location similarly in magnitude. Additionally, the touch location main effect was not significant (F (7, 49) = 2.23, p = 0.11), suggesting that the magnitude of the effect was the same across touch locations. However, a significant interaction of touch location by head position was found (F (7, 49) = 5.75, p = 0.013). As can be seen in Figure 3.1b, head position had a larger effect on touches that were located on the same side of space. Thus, when the head was positioned to the left the touches on the left were affected more (M = 11.3 mm left tactors, M = 6.0 mm right tactors) and when the head was positioned to the right the touches on the right were affected more (M = 16.0 mm right tactors, M = 8.7 mm left tactors).

We hypothesized that holding the head eccentrically for several minutes might lead to some kind of adaptation, which might affect the coding of touch location. Therefore, we calculated correlations between the perceived position of touch and the time in seconds since the participant had began that head condition. Pooling across and controlling for touch location, no evidence for a drift in perceived position of touch was found for either left (r (766) = -0.009, p = 0.80) or right (r (766) = 0.055, p = 0.13) head positions.

Experiment 2

The localization data from Experiment 2 where the head returned to center before the response was made is plotted in Figure 3.1c. These data were analyzed using a two-way repeated-measures ANOVA. A significant effect of tactor location (F

(7, 49) = 244.83, $p < 0.001$) confirmed that touch location could be discriminated. A significant effect of head position (F (2, 14) = 17.36, $p = 0.004$) indicated that the perceived position of a touch was affected by head position. As in Experiment 1, the effect of head position was found to be linear (F (1, 7) = 17.82, $p = 0.004$), indicating that left and right head positions affected perceived touch location equally in magnitude but opposite in direction. Touches were perceived furthest to the left when the head was positioned to the left (M = 1.13 cm left), more medially when the head was centered (M = 0.11 cm left), and to the right when the head was right (M = 1.06 cm right). A significant interaction of head position by touch location was found (F (14, 98) = 8.57, $p < 0.001$), indicating that the effect of head position was different at the different touch locations. This effect is further explored in the analysis of the difference-from-center data (Figure 3.1d)

The unsigned difference data were subjected to the two-way repeated-measures ANOVA. The main effect for head location was not significant (F (1, 7) = 2.31, $p = 0.17$), indicating that the size of the head orientation effect was equal for the left (M = 1.14 cm) and right (M = 1.34 cm) head orientations. A main effect of tactor location indicated that the effect of head position was different depending on the location of the touch (F (7, 49) = 6.29, $p = 0.003$). The head position by touch location interaction was also significant (F (7,49) = 9.06, $p = 0.002$). This indicated that touches on the same side as the eccentric head position were affected more (head left, left touches M = 1.62 cm; head right, right touches M = 1.94 cm) than those on the opposite side (head left, right touches M = 0.66; head right, left touches M = 0.74 cm).

Experiment 1 and 2 Discussion

The results of Experiment 1 replicate Ho and Spence (2007), showing that when touches are localized under eccentric head conditions the perception is shifted in the opposite direction of head eccentricity. The results of Experiment 2 are consistent with the results of Pritchett and Harris (2011), demonstrating that when a touch is applied under eccentric head position but reported under centered head position the perception is shifted in the same direction of head eccentricity.

We can therefore conclude that the opposing results are not due to the different body parts tested (torso vs. arm) or to the type of touch stimuli used (vibration or tap). We can also rule out adaptation affects during the blocked head condition trials of Experiment 1 as no systematic drift in perceived touch location was found across time.

Other differences between the two procedures are that the scale used for response in Experiment 1 was viewed with the head-eccentric and that it was necessary to remember and update the location of the touch after moving the head in Experiment 2. Experiment 3 was therefore designed to test the possible contribution of these two factors. In Experiment 3, touches were delivered while the head was centered, but the response was made with head-eccentric; thus, the scale was viewed with head-eccentric (as in experiment 1), and it was necessary to remember the location of the touch during a movement (as in experiment 2), but the touches were delivered with the head and eyes centered.

Experiment 3

Participants

Eight participants (4 males, 4 females, mean age 28 years) completed Experiment 3. Five of them had also completed both Experiments 1 and 2.

Method

Participants were arranged with their body pointing either to the left, right, or straight toward the screen for each block of trials. In conditions where the participant was not facing the monitor, an LED was placed directly in front of the participant as a fixation point; when facing the monitor a cross displayed on the screen was used. To begin each trial the central fixation point and the head-mounted laser were illuminated and participants aligned their eyes and head with this point. After 2 seconds the fixation and head- mounted laser were turned off, and a touch was presented from a randomly chosen tactor on the array. Next, the laser and a fixation cross on the computer monitor were illuminated. Participants were given 2 seconds to align the head laser with the fixation cross. Next the visual scale was displayed on the screen. The participant reported the perceived location of the touch on the scale and clicked the ‘‘OK’’ button. This triggered the beginning of the next trial. The participant turned their head back to the centered location and aligned the laser and their eyes with the fixation point ready for the next trial. Each of the 8 tactors was presented 12 times before the block terminated in approximately 7 minutes The chair was then repositioned, and the next head condition was run until all three had been completed. Conditions were counterbalanced across participants.

Results

The localization data from Experiment 3 are plotted in Figure 3.1e, f and were analyzed using a two-way repeated- measures ANOVA. The main effect of touch position was significant (F (7, 49) = 539.10, p < 0.001), indicating that the touches could be discriminated. The main effect of head position was not significant (F (2, 14) = 2.56, p = 0.12), indicating that the touches were perceived similarly regardless of the position of the head at the time when the location was reported. Finally, the touch location by head position interaction was not significant (F (14, 98) = 0.77, p = 0.54). These results indicate that there was no effect of head position on the response. This suggests that there were no effects of eccentrically viewing the scale in Experiment 1 or of moving the head in Experiment 2.

General Discussion

The experiments described here confirm that there is a systematic effect of head position on perceived touch location and that this depends critically on the procedure used to measure it. We have successfully reproduced the effect of shifting touch in the opposite direction of eccentric head position when following the procedure of Ho and Spence (2007). And we replicate the effect of shifting perceived touch location in the same direction as head position when following procedures more similar to Pritchett and Harris (2011). The present experiments allow us to rule out some explanations for the opposing effects. The difference is not simply due to type of touch (vibration or tap) or to the body part tested (torso vs. arm). We can rule out adaptation effects during the blocked head condition trials of Experiment 1 as no systematic drift in perceived touch location was found across time. Finally, the null results of Experiment 3 demonstrate that the difference cannot be simply explained as resulting from eccentric viewing of the scale in Experiment 1, or from moving the head in Experiment 2. This indicates that the results are not due to spatial updating. If the results were due to spatial updating then in Experiment 3 where touch was presented with head centered and reported with the head turned the localization response would have been different than when touch was presented and reported with head centered. Instead, the results point to different mechanisms for encoding, storing, or retrieving touch location in the two experimental situations.

Lewald & Ehrenstein (1996a) argued that auditory localization was only found to move in the direction opposite to gaze when a visual reference was used and that the effect of gaze on visual localization was larger than it was on auditory. This combination can, therefore, make it appear as if auditory localization is shifted in the same direction as gaze because of the opposing effects of gaze on the sound stimulus and on the visual reference used to measure it. Our control study rules out effects of the probe scale as an important contributor to the results reported here. We offer another explanation for opposite effects of gaze on the perceived location of touches in different situations.

Why are Gaze-Induced Localization Errors Found in Opposing Directions?

Holding the eyes eccentrically shifts the perceived body straight ahead in the same direction as the eyes (Harris & Smith, 2008; Hill, 1972; Morgan, 1978). Similar results have also been found when the head, rather than the eyes, is held eccentrically (Yamaguchi & Kaneko, 2007). That is, the angle between the body and eye straight ahead is underestimated. As shown in Figure 3.2a, an underestimated representation of gaze eccentricity can be described as perceiving the body straight ahead as shifting toward gaze. That is, in the same direction as head position (as in Hill, 1972 Experiment 2 and 3). Or, it may be regarded as the location of gaze moving closer to the actual body. That is, a shift in the direction opposite to head position (as in Hill, 1972 Experiment 4). Thus, which direction the perceived touch location shifts may be dependent on the frame of reference (body or gaze) to which it is attached.

As shown in Figure 3.2b, if the body midline were shifted in the same direction as head position, any location coded relative to body midline would show errors in the direction opposite to head position. In contrast, Figure 3.2c shows that if perceived gaze were shifted in the opposite direction of head position, then any stimulus coded relative to gaze would show errors in the same direction as eccentric position. We therefore conclude that the opposing effects of gaze eccentricity described here may be the result of coding stimuli relative to the body in Experiment 1 and relative to gaze in Experiment 2.

This explanation is consistent with work in the auditory domain. Numerous reports exist of auditory perception shifting in the direction opposite to gaze

(Kopinska & Harris, 2003; Lewald & Ehrenstein, 1996a, 1996b, 1998). The explanation offered for this shift has been that it is linked to a shifted perceived median of the head. When participants were asked to adjust a dichotic sound until it sounded as if it were in the middle of the head while their eyes (Lewald & Ehrenstein, 1996b, 1998) or head (Kopinska & Harris, 2003; Lewald & Ehrenstein, 1998) were turned, participants consistently adjusted the sound such that it was more intense in the ear on the same side as gaze. This indicated that they perceived the sound as shifted in the direction opposite to gaze.

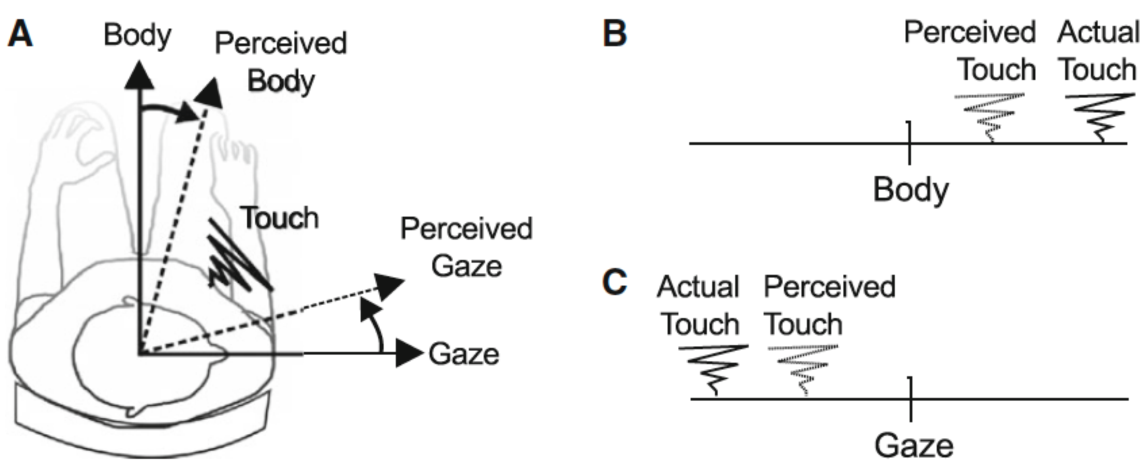

Figure 3.2. Model of how an eccentric head position may shift perceived touch location in either the same or opposite direction as head position. Solid lines represent accurate locations, dashed lines represent perceived locations (of body and gaze in a and of touch in b and c). A: Illustrates different consequences of an underestimated gaze angle. The perceived body center is shifted toward gaze and perceived gaze is shifted toward the body (see text for details). B: The result of coding relative to a shifted body midline is that the perceived location of touch is shifted in the direction opposite to head position. C: The result of coding relative to a shifted gaze direction is that the perceived location of touch is shifted in the same direction as head position.

Mechanism

Touch location is initially coded by a labeled-line system where the nerve endings in the skin transmit information to the primary somatosensory tactile homunculus. If the conscious perception of touch arose from that representation, then no systematic errors related to gaze position would be expected: perceived touch location should correspond directly to actual touch location. However, the parietal cortex contains many spatial representations that are responsive to tactile as well as visual and auditory stimulation (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Cohen & Andersen, 2002; Galati, Committeri, Sanes, & Pizzamiglio, 2001; Mullette-Gillman, Cohen, & Groh, 2005; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). These multisensory maps are thought to code space in different coordinate systems. For example, the lateral intraparietal area (LIP) of the monkey seems to code space not only in an eye-centered representation but also relative to head-centered and intermediate reference frames (Mullette-Gillman et al., 2005; Stricanne, Andersen, & Mazzoni, 1996), while the ventral intraparietal area (VIP) seems to code space in a body-centered representation (Sereno & Huang, 2006). Converting touch information from a body representation into head, eye, or gaze frames requires taking eye and head position into account. Inaccuracies in the representation of head, gaze, or eye position thus get passed along as tactile space is converted into such a frame.

Why are our Effects Asymmetrical?

A noticeable feature of our data is the asymmetry of the effects on the left and right sides of the body (Figure 3.1b, d). When the head was turned to the left the touches on the left side of the body were more affected, and when the head was turned to the right the touches on the right side of the body were more affected. This is true for both Experiment 1 and 2 as can be clearly seen in the data of Figure 3.1a, b. It seems that only the touches on the same side of the body as the direction of gaze are affected. When interpreted in the context of the frame conversion model, this might suggest that only touches within the current visual field are recoded relative to the body midline or gaze. The non-affected touches, which are outside the visual field, may remain coded in the original somatotopic reference frame. This is consistent with other work showing that vision affects coding of touch location (Haggard, Christakou, & Serino, 2007; Kennett, Taylor-Clarke, & Haggard, 2001; Sathian & Zangaladze, 2002; Tipper et al., 2001). Another possibility is that touches on the side of the body opposite to gaze are coded in both gaze- and body-centered coordinates simultaneously with equal weighting. In that case, the opposite-directed errors could cancel out.

Conclusion

The results of the experiments described here suggest that perceived locations of tactile stimuli are coded differently depending on the situation. In the static design of Experiment 1 and Ho and Spence (2007), touch location may be coded relative to the body, while in the more dynamic conditions of Experiment 2 and Pritchett and Harris (2011), touch may be coded relative to gaze. This may be connected to using a more centralized, gaze-centered reference frame when the locations of touches need to be remembered and reconstructed after a move. These findings may have important applications in designing working environments, as spatial representations may be different depending on context and task demands. Drivers, pilots or users of backhoes, for example, may interpret the location of tactile objects differently depending on the situation and where they are looking. These findings may improve our understanding of the different patterns of spatial neglect that are seen in parietal brain damage patients attempting different tasks (see Colby, 1998) and may have implications for the blind.

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Chapter 4. The Effects of Gaze on the Perceived Location of Touch on the Back

Abstract

The direction of gaze affects the perceived location of touch on the arm and on the front of the torso, suggesting an at least partial coding of touch in a visual reference frame. Might parts of the body that cannot be seen also be coded visually? Here we present touches to the lower back and look for effects of eccentric gaze (head oriented at 90° on the body, with eyes centered in head) on their perceived locations as clues to the coding mechanisms involved. We use two different procedures: dynamic and static. In the dynamic task the participant held an eccentric head position for touch presentation and returned to center to respond. This has been suggested previously to elicit gaze-centered coding. The static task, in which the head remained eccentric throughout, has been suggested as being associated with body-centered coding. Perceived location was measured on a visual scale referenced to a tactile array. During the static task, the shift in the perceived location of touch on the back was smaller than previously found for touch on the front, or in the dynamic task for stimuli on both the front and back, indicating a more stable representation of touch location. For the dynamic procedure, the perceived location of touch on the side of the back to which the head was turned shifted towards that side of the body, that is rotated around the body in the opposite direction to that reported for touch on the front under the same conditions. These observations are

discussed in terms of task-based reference frame transformations and the relationship between the front and back of the body.

Introduction

We consider our bodies as having a distinct front and a back. However, this distinction may not be reflected in the representation of our body in our brains. The body representation is built up from information from multiple sensory systems, including vision and the somatosensory systems, and incorporates proprioceptive information about the body's posture. Vision makes us familiar with the front of our bodies (from an egocentric perspective), while the back of our own body is rarely if ever viewed. If there is a visual representation of the back of our body it must be built up from visual experience of the bodies of others, by imagination, or by occasional views of our own body when it is glimpsed in a mirror. Additionally, we could use what we know about the front of our body to predict the size and shape and relative position of our back.

Touch localization relies on a representation of the body, its size and shape and knowledge of the density of receptors in the skin (Longo & Haggard, 2012; Taylor-Clarke, Jacobsen, & Haggard, 2004). Visual information provides the best metric for the size of our bodies, so an important question is whether reference frames for coding touch location on the front (visible) and back (nonvisible) of our body are the same. A mental representation known as the body schema maintains the spatial relationships between body parts and is also involved in localizing tactile stimuli in space (Medina & Coslett, 2010). The initial somatotoptic information about touch locations (from receptors in the skin) must be integrated with the body schema in order to predict where the touch location occurred. Single cell recording (see Cohen & Andersen, 2002) and brain imaging (Bernier & Grafton, 2010) have established that the brain uses a continuum of reference frames for coding spatial locations. Body landmarks may provide natural reference points within each of these frames to help localize tactile stimuli. Indeed, localization is more accurate when touch is delivered near a landmark (such as the nose, wrists, elbows, navel, or spine) (Cholewiak, Brill, & Schwab, 2004; Cholewiak & Collins, 2003). These reference frames may also use egocentric directions (such as body-straight-ahead or gaze-direction) as reference points for coding stimulus locations (Colby & Goldberg, 1999). The posterior parietal cortex in humans has been shown to be causally involved in transforming between the initial somatotopic representations of touch and the higher-level egocentric representations (Azañón, Camacho, & Soto-Faraco, 2010).

Most researchers have investigated the localization of touch presented to the arms (Cholewiak & Collins, 2003; Harrar & Harris, 2009, 2010; Pritchett & Harris, 2011), hands (Azañón & Soto-Faraco, 2008; Longo & Haggard, 2012) or the front of the torso (Cholewiak et al., 2004; Pritchett, Carnevale, & Harris, 2012). Here we extend these studies to include the back. We have previously found that touch on the front of the body is mislocalized when gaze is directed to one side. However, this displacement is in opposite directions depending on the task (Pritchett et al., 2012). To explain this, we turn to previous research which has demonstrated that the brain systematically misestimates both the perceived gaze direction and the body-straight-ahead. These directions are misperceived toward one another when gaze is eccentric: the perceived body-straight-ahead is shifted in the direction of gaze, and the perceived direction of gaze is underestimated and perceived as closer to the body-straight-ahead (Harris & Smith, 2008; Hill, 1972; Morgan, 1978; Yamaguchi & Kaneko, 2007) (see figure 4.1A and C). If touch locations are systematically referenced to one or other of these depending on the task, it could explain the directions of gaze-related shifts previously reported (Ho & Spence, 2007; Mueller & Fiehler, 2014; Pritchett et al., 2012), and provide a tool for determining which reference frames are used to code touch localizations during various tasks. Pritchett et al. (2012) and Mueller and Fiehler (2014) conclude that whenever effectors (head, eyes, limbs) are held static, a predominately body-centered representation is used for tactile localization. While when effector movement is required between perceiving and responding, a gaze-centered representation is used. Whenever effectors move, the representation of their locations must be updated. Additionally, any locations coded relative to those effector reference points also require updating. It seems that a gaze-centered reference frame is commonly used for updating spatial locations of all modalities, including touch. But, will a gaze-centered representation still be used for the lower back, a part of the body not typically seen?

In a static task where no gaze shift is required between touch presentation and response, we expect that touch will be coded in a body-centered reference frame, in line with previous research (Bernier & Grafton, 2010; Mueller & Fiehler, 2014; Pritchett et al., 2012). Based on our model of how gaze eccentricity affects the perceived location of reference points (Figure 4.1), we would expect body-centered coding to be associated with shifts in the perceived location of touch in the opposite direction to that in which the head is turned. That is, assuming a three-dimensional model of the body, leftward gaze would lead to clockwise rotation of the perceived locations around the body and rightward gaze would lead to counter-clockwise rotation, (see Figure 4.1A and B).

In a dynamic task participants are presented with a touch while their head is eccentric (evoking misperceptions of reference points that the touch is coded relative to) and then turn their head to center before reporting the touch location. This task is expected to utilize a gaze-centered reference frame consistent with previous findings (Mueller & Fiehler, 2014; Pritchett et al., 2012). Based on our model (Figure 4.1) we would expect this to be associated with shifts of perceived touch location in the same direction as eccentric gaze (Figure 4.1C and D). That is, to rotate around the body in the opposite direction to the static condition. Such shifts would indicate that a gaze-centered reference frame is available for spatial locations behind the body. Another possibility is that touch location on the back may always be coded in a body-centered reference frame. If this were true we would expect to find the same pattern of gaze-related errors in the dynamic and static conditions.

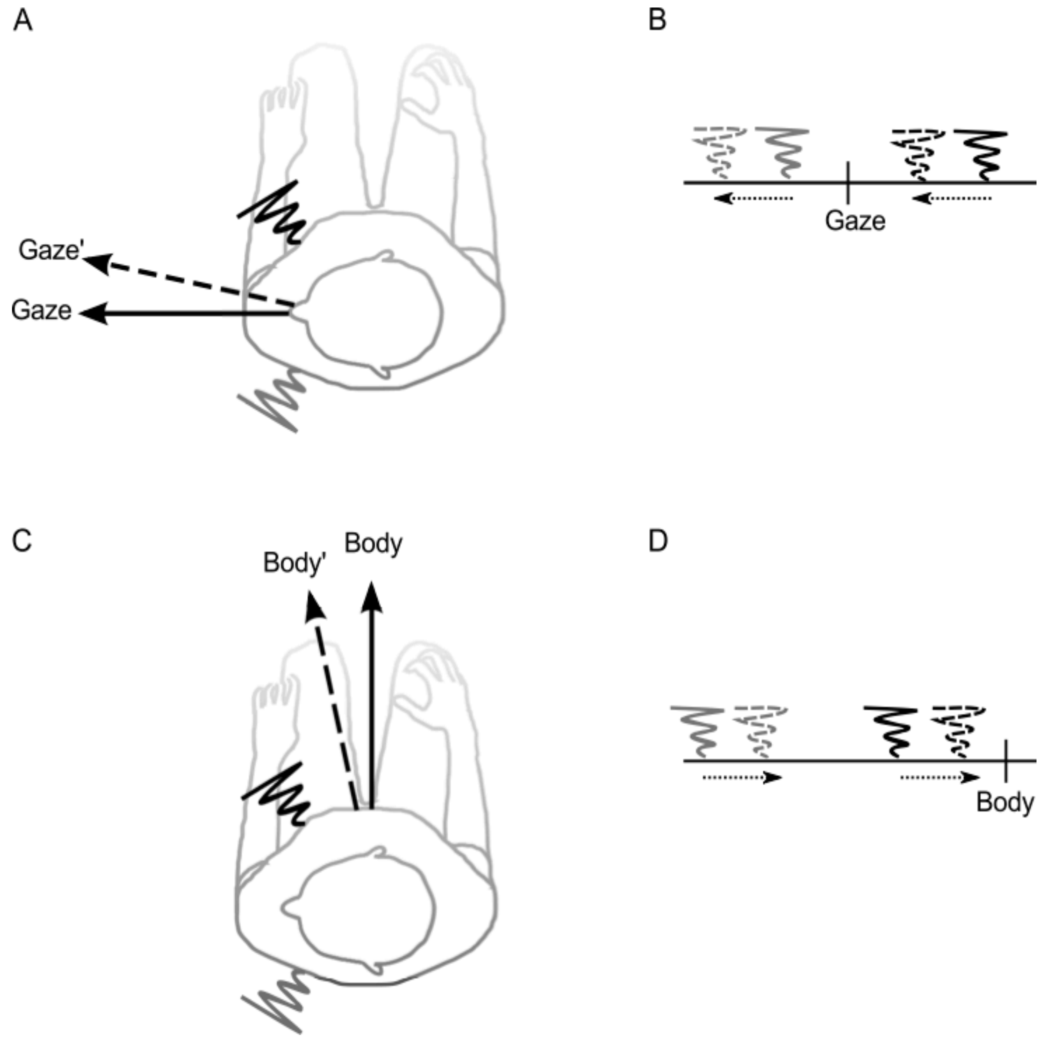

Figure 4.1. Illustration of how coding touch location relative to an underestimated representation of gaze (A and B) or a shifted body-straight-ahead (C and D) can result in oppositely directed gaze-related errors. Touch locations are represented by zigzags. Actual directions and locations are shown by solid lines; perceived directions and locations are represented by dashed lines. During eccentric gaze, perceived gaze direction (gaze') is underestimated (A). Simultaneously perceived body-straight-ahead (body') shifts toward the direction of gaze (C), B and D represent gaze-centered and body-centered reference frames respectively. If the location of a touch on the front or back were referenced to the perceived gaze direction (gaze') rather than the actual gaze direction it would be perceived as closer to the direction of gaze than it actually was: that is, it would be displaced in the same direction as the head was turned (B). If that same location were referenced to the perceived body-straight-ahead (body'), it would be perceived as closer to the body-straight-ahead than it actually was: that is it would be displaced in the opposite direction to that in which the head was turned (D).

Method

Participants

Ten participants (5 female, average age 26 years) gave informed consent and completed both experiments in separate sessions. Procedures were approved by the York Ethics board and conformed to the declaration of Helsinki.

Apparatus

Tactor display. Eight tactors (Engineering Acoustics, model C2) were attached in a linear array to a Velcro belt with a separation of 4 cm between each tactor (thus the extent of the array was 28 cms). The belt was worn around the waist, just below the level of the navel, over the participant's shirt, with the tactor array centered on the spinal vertebrae. The tactor array extended horizontally across the lower back. Tactors were labeled 1-8 with tactor 1 always on the left side. This convention was also used for previous experiments where the tactor belt was worn on the front (see data figures below). It is thus important to note that 1 to 8 corresponds to a clockwise direction on the front, but a counter clockwise direction on the back. Vibrotactile stimuli (250 Hz, 50 ms duration) were generated by a PC, amplified by an audio amplifier, and delivered to a particular tactor in the array through a custom-made computer-controlled system of relays. Stimuli were of one of four intensities (37.5, 50, 62.5, 75% of maximum intensity), randomly chosen to keep participants from identifying a given tactor by using any subtle intensity differences between them. All intensities were well above threshold, in the "light touch" range. Headphones were used to present white noise to cover the sound of the tactor vibrations.

Eye and head position. To guide head position, a laser pointer was mounted on a baseball hat worn by the participant pointing straight ahead. Participants pointed the beam and looked at target LEDs or points drawn on a computer screen. The gaze/head orientations tested were 90° left and right and straight ahead (eye position was always centered in the head). In the static procedure (Fig. 2 A-C), participants were oriented such that the computer screen was either 90° to their left, 90° to their right, or straight ahead of their body. In the dynamic procedure (Fig. 2D), participants were initially oriented so that their head and body pointed straight-ahead toward the computer monitor. Target LEDs were placed 62 cm from the participant at 90° to their left and right to indicate where they needed to point their head and eyes during stimulus presentation. Head and eye orientation was self-monitored by the participant as all that was required was a large gaze shift to one or other side. Small deviations of gaze from the targeted eccentricities would have had no appreciable effect on the data.

Measuring perceived touch location. For reporting the perceived location of the touch, a horizontal white bar measuring 35.3° of visual angle was displayed on the screen (after Ho & Spence, 2007 and Pritchett et al., 2012). A small rectangle (cursor) was drawn at the center of the bar that could be moved by clicking on the screen or could be dragged by a mouse. Participants adjusted the position of the cursor to indicate the perceived location of each touch. Participants were instructed that the line represented the extent of the tactile array and that each end represented the location of the tactors at the end of the array. The position of these "marker tactors" was demonstrated by vibrating them before each experiment.

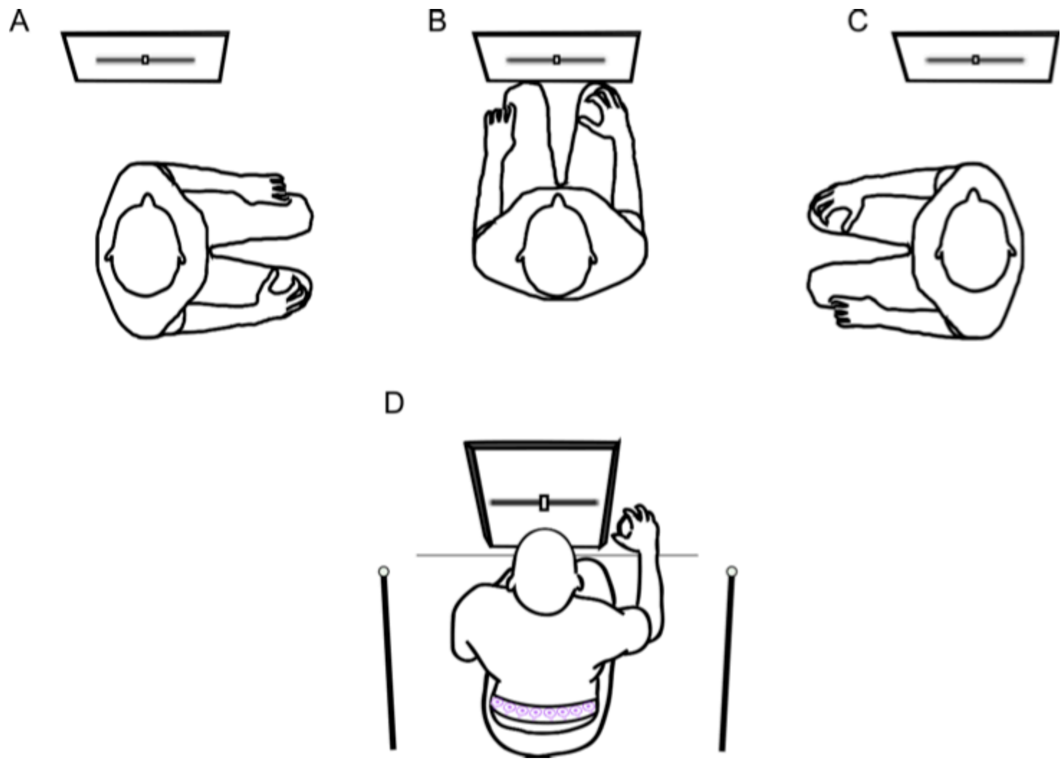

Figure 4.2. Illustration of how participants were arranged in the apparatus in the static (A, B, and C) and dynamic condition (D). In the static condition, participants were arranged such that the response scale was to their left (A), center (B), or right (C) and their head was oriented towards the scale for the duration of the trial. In the dynamic condition (D), participants were initially seated facing the response scale as shown. On each trial they were directed to orient their head either to the left, center, or right, guided by the target LEDs shown. While there, a touch was presented from the tactor array; they then returned their head to the straight ahead to report the perceived touch location on the scale. Locations were always reported on a visual line (shown here on each screen) such that the furthest left part of the line represented the furthest left tactor and the furthest right part of the line represented the furthest right tactor on the array

Procedure. Participants completed the static and dynamic procedures on separate days. In the static condition (Figure 4.2 A-C), subjects held their head and gaze in the same orientation for the duration of all trials (head left, centered, or right). For the dynamic condition (Figure 4.2 D), participants were directed to orient their head and gaze to the left, center, or right (randomly chosen) on each trial. The touch was delivered while they were in that orientation and then they then re-oriented their head to the center before reporting the touch location on the visual scale displayed on the screen in front of their body.

Static procedure. Participants were helped to wrap the Velcro strap with the tactor belt around their body and to center the array on their spine. They then put on the laser hat and headphones. The chair was positioned such that participants had to orient their heads 90° to the left, right, or straight ahead on their body to view the computer monitor. Participants were seated and each of the tactile stimuli was demonstrated. They were asked to remember the locations of the tactors on each end of the array and map them onto the ends of the visual scale.

Each trial began with a fixation cross on the screen. Participants pointed the head-mounted laser at the cross and fixated it with their eyes. The vibrotactile stimulus was then applied to a randomly chosen tactor from the array. Five hundred milliseconds later the response scale was drawn on the screen. Participants reported the perceived location of the vibration using a mouse to adjust the position of the gray rectangle on the visual scale and clicked an “OK” button when satisfied with the report. Their response triggered the next trial. Each of the eight tactors was presented 12 times for a total of 8 x 12 = 96 trials requiring approximately 7 minutes for each head orientation. Next, the experimenter rearranged the chair to the next position and the next block of trials was run until all three conditions (head left, right, or center, in counter-balanced order) were completed.

Dynamic procedure. Participants were seated in the center of the apparatus directly in between the two head fixation LEDs with the computer monitor straight ahead. The head laser was illuminated and participants pointed it at the central head fixation point. A set of ten practice trials was then presented in random order before the full experiment commenced so that participants could get a feel for using the bar to report the perceived position of a touch and get comfortable with moving the head laser to the various head fixation targets.

Each trial began by illuminating the head laser and a head fixation point. If it was the straight-ahead condition, a cross was drawn on the screen. If it was a left or right head orientation condition, the appropriate LED was illuminated and an arrow was drawn on the screen pointing in the appropriate direction. The participants were given 2 seconds to align the head laser and their eyes with the fixation point. Once in position, a vibration was applied from a randomly chosen tactor in the array. After presentation of the touch, the participants turned their heads back to center and viewed the visual scale. The participant indicated the perceived location of the vibration using the mouse, clicked the “OK” button, and the next trial was triggered. The experiment was conducted in one approximately 30-minute session with the trial order randomized. Each of the eight tactors was presented 12 times for each gaze condition resulting in 8 x 12 x 3 trials = 288 trials.

Data Analysis. Participants' responses on the visual scale were coded between 0 and 1 where 0 represented the furthest left part of the line (and the furthest left touch) and 1 represented the right part of the line (and the furthest right touch). Results were converted into centimeters by multiplying the response data by 28 cm (the extent of the tactile array) and subtracting 14, so that responses were coded as the distance from the center of the tactile array. For each condition, the average perceived location of each tactor for each gaze orientation was calculated for each participant.

Results

Figures 4.3 and 4.4 show the average perceived location of each of the eight tactors presented while the head was left, center, and right for the static and dynamic conditions respectively. In both Figures, the left panels (A and B) show data redrawn from Pritchett et al. (2012) where touch locations were delivered to the front of the body using the same procedure described here. The right panels (C and D) show the localization data when touches were presented to the back. The top panels (A and C of Figure 4.3 and 4.4) show where touch locations were perceived with the head left, center, and right. The bottom panels (B and D of Figure 4.3 and 4.4) show the difference between where touch locations were perceived with the head centered and with the head eccentric. These difference-from-center data show the effect of head position on touch localization, which is the main interest here.

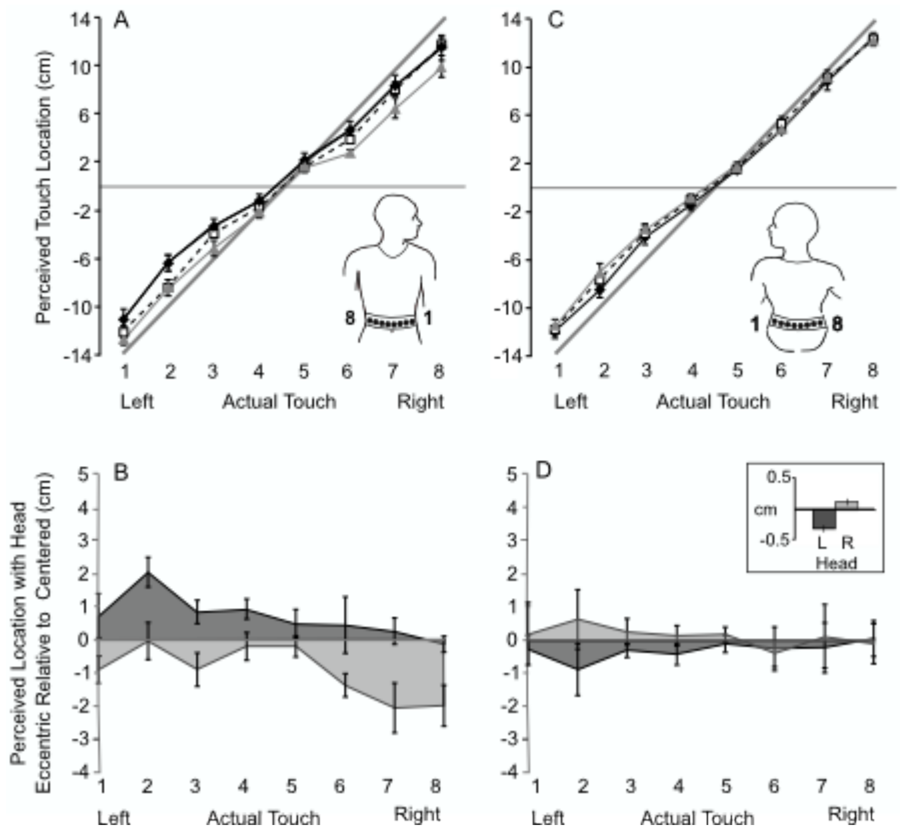

Figure 4.3. Results from the static condition. A and C: Average perceived touch location (measured in cm from the body-center by converting the average location marked on the visual line to the extent on the tactile array) of the eight tactors (numbered sequentially from the participant's left to right) for each of the three gaze conditions (head left dark diamonds and black line; head center, black open squares and dashed line; head right, light triangles and gray line) for touches on the front (A) and back (C). Also shown is the straight line estimating accurate perception. B and D: the difference between the perceived location of each touch with head left (dark shaded area) or right (light shaded area), and their perceived locations with the head centered for touches on the front (B) and back (D). D includes an inset histogram illustrating the main effect of head orientation averaging across all touch locations. Error bars show SEM, except the inset of D, which uses within-subject SEM (Cousineau, 2005). Data in panels A and B redrawn from Pritchett et al., 2012.

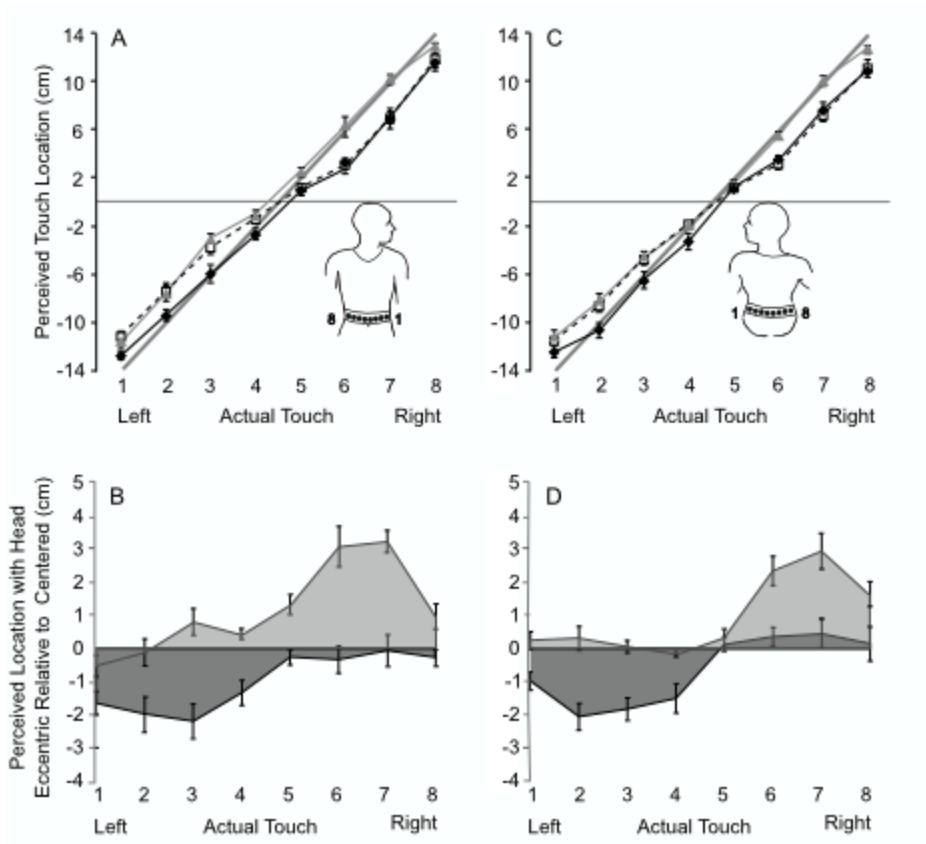

Figure 4.4. Results from the dynamic condition. Format is as for Fig. 3. Error bars are SEM. Data in panels A and B redrawn from Pritchett et al. (2012).

The touch localization on the back data (Figures 4.3C and 4.4C) was submitted to a three-way repeated measures ANOVA for effects of procedure (static vs. dynamic), head orientation (90° left, center or 90° right) and touch location (8 target locations across the lower back). The three-way interaction was significant (F (14, 126) = 2.56, p = .02, *partial eta sq* = .22), so the effects of head orientation and touch location were analyzed for the static and dynamic procedures separately.

Static Procedure

For the static procedure (Figure 4.3 C and D), head orientation had a significant effect on perceived touch location on the back (F (2, 18) = 3.82, p = .046, *partial eta sq* = .30). Head position and touch location did not show a significant interaction (F (14, 126) = 0.70, p = .58) meaning that head orientation affected all touch locations in a similar manner. On average, when the head was oriented to the left during presentation of the touch, touch was perceived 0.44 cm further to the left than when the head was oriented to the right (see inset in Figure 4.3D) (t (9) =-3.52, p = .007).

Dynamic Procedure

For the dynamic procedure (Figure 4.4C and D), touch location and head orientation had a significant interaction with perceived touch location on the back, indicating that the effect of head orientation differed depending on the tactor location (F (14, 126) = 8.23, p < .001, *partial eta sq* = .48). All touch locations except for number 5 (the tactor 2 cm to the right of the spine, F (2,18) = 1.14, p = .34) showed a significant effect of head orientation (all F (2, 18) > 8.00, all p < .01). Moreover, paired t-tests showed that when the head was at 90° left during presentation of the touch, perceived locations of all tactors except location 5 (t (9) = 0.95, p = .36) were further to the left than when they were presented with the head to the right (all t > 2.97, all p < .02). The difference between perceived locations with head left and head right was 1.85 cm on average (excluding tactor 5).

Inspection of the graphs for the dynamic condition (Figure 4.4D) show that touches on the side towards which the head was displaced were more affected than those on the other side. This is also supported by the interaction of head orientation and touch location reported above.

When the head was oriented to the left during presentation of the touch, the perceived locations of the tactors on the left of the spine (1-4) were significantly different from their perceived locations when the head was centered (all t (9) > 3.43, all p < .007). For these tactors, the perceived locations with head left for presentation of the touch were on average 1.60 cm to the left of where they were perceived with head centered. Touch locations to the right of the spine (5-8) were not significantly shifted when the head was to the left for presentation of the touch compared to centered (all t (9) < 1.34, all p > .21).

When the head was oriented to the right during presentation of the touch the perceived locations of tactors 6, 7, and 8 (on the right of the spine) were significantly different from where they were perceived to be with head centered (all t (9) > 4.30, all p < .003). These tactor locations were perceived on average 2.34 cm to the right compared to where they were perceived with head centered. The other five tactor locations (1-5) were not significantly affected by having the head to the right for presentation of the touch (all t (9) < 1.61, all p > .14).

Comparing Static and Dynamic Procedures

The static procedure had a relatively small effect compared to the dynamic procedure and compared to previous results from Pritchett et al. (2012). Several factors could help explain why. Holding the head eccentric over time could result in an adaptation of the perceived straight-ahead. To examine this, we computed the correlation of perceived location and time. We found no evidence of a shift in perceived location over time, the partial-correlation (pooling over and controlling for participant and touch location) between touch localization and time of response was nearly zero for both head left (r (958) = 0.059, p > .05) and right (r (958) = 0.003, p > .05) conditions.

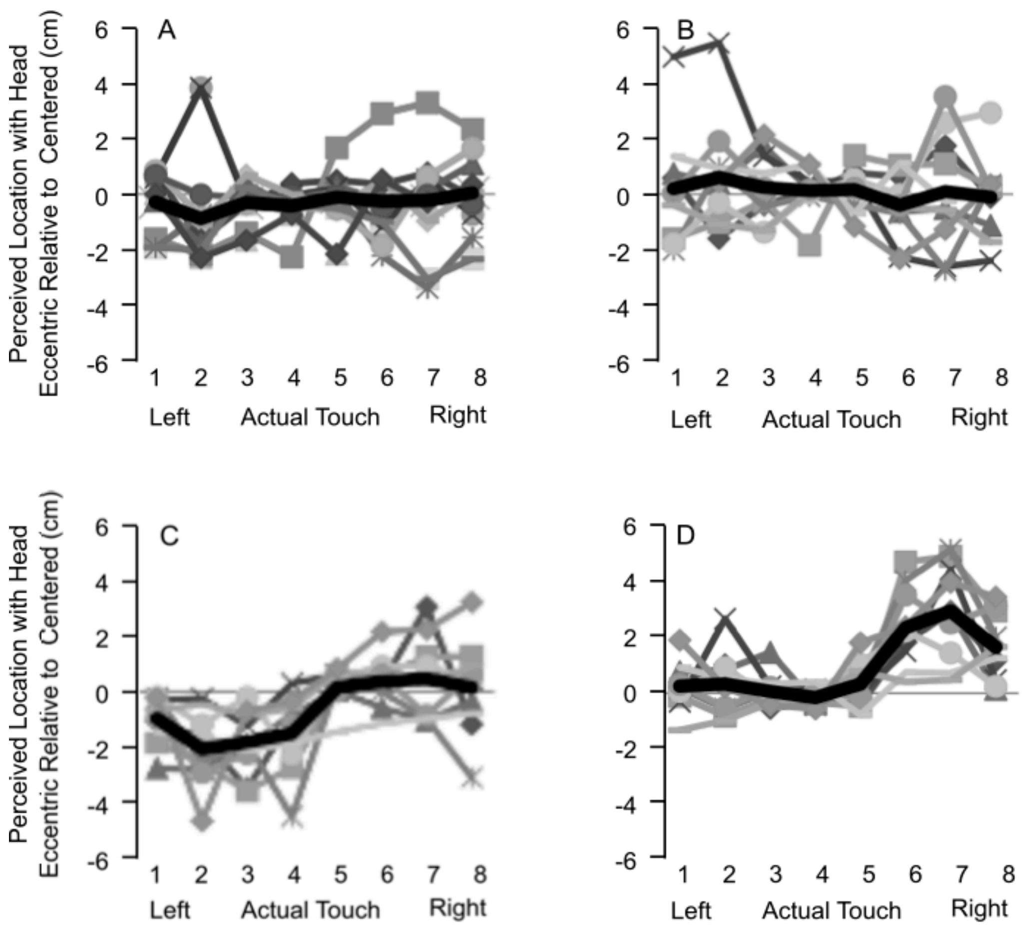

Figure 4.5. The perceived location of touch on the back with the head eccentric relative to when the head was centered plotted for each individual subject in the static (A and B) and dynamic (C and D) conditions, with the average shown in bold. The left panels (A and C) show effect of head left and the right panels (B and D) show effect of head right.

Another possible explanation for the smaller average effect in the static condition is increased between-subject variability. Increased between-subjects variability could indicate that participants used different strategies during this task. To examine this the effect of head position (using the head-centered condition as a baseline) for each participant is plotted in Figure 4.5 for the static (Figure 4.5A and B) and the dynamic condition (Figure 4.5C and D). In the dynamic condition, all participants show effects remarkably consistent with the average (bold line), whereas in the static condition, the data appear noisier. To quantitatively assess whether there was more between-subject variability in the static condition compared to the dynamic condition, the between-subject variability in the effect of head position across subjects was calculated for each touch location in the dynamic (M = 0.076, SD = 0.05) and static (M = 0.050, SD = 0.033) conditions and were found to be not significantly different (t (30) = 1.67, p > .05). Together, these analyses allow us to conclude that the smaller effect found in the static condition is not the result of either adaptation, or multiple strategies. Instead, we find that there is truly less effect of head orientation on touch localization in the static task compared to the dynamic task.

Discussion

Similar to previous findings on the front of the body, touch localization on the back was found to depend on the orientation of the head during presentation of a touch. As for the front (Ho & Spence, 2007; Pritchett et al., 2012), details of the effect on the back depended on the experimental procedure used. When head position was held eccentric for an entire block of trials for both touch presentation and response (static condition), there was a small but significant shift of touch locations towards the side of the body to which the head was turned. When participants oriented their head eccentric for presentation of the touch but returned to center to respond (dynamic condition), touch localization showed a large shift, also towards the side of the body to which the head was turned. Again similar to results on the front, this effect was only found for touch on the side of the body to which the head was turned. That is, touch on the left side of the back was only affected by leftward head displacement and touch on the right side of the back was only affected by rightward head displacement.

These results are not consistent with the predictions based on a solid 3D model described in the introduction and illustrated in Figure 4.1. Those predictions were that for both the static and the dynamic condition the perceived location of touches on the back of the body should rotate around the body in the same direction as they did on the front. Thus, clockwise shifts would be associated with rightward movement on the front and leftward movement on the back and visa versa. For the static task this was somewhat true, the perceived location of touch on both the front and back of the body rotated around the body counterclockwise for rightward head movements (leftwards on the front and rightwards on the back) and visa versa. However, the shift of the perceived location of touch on the back of the body (0.44 cm) was only a fraction of what was found on the front of the body (1.63 cm). Additionally, the pattern of shifts found on the back differed from the typical pattern of shifts in which the effect is only present on the side of the body to which the head is turned (see Pritchett et al., 2012; Ho and Spence, 2007).

For the dynamic task, clear, systematic gaze-related shifts of the perceived location of touches on the back of the body with the typical pattern of distribution along the tactor array were seen comparable to those on the front. However, while the dynamic task was associated with the perceived location of touches on the front being displaced in the direction of gaze (Figure 4.4B), here the displacement was in the opposite direction (a leftward head movement evoked counter-clockwise shifts on the front but clockwise on the back and visa versa). The magnitude of the effects were similar (mean 2.19 cm for front, mean 1.64 cm for back), and for both touch on the front and back shifts were only found for touches presented on the side of the body to which the head was turned.

Static task

We expected that the static task would be associated with a body-coding system with errors related to the displacement of the perceived body-straight-ahead (Figure 4.1C and D). The direction of displacement of the perceived location of touch on the back was consistent with this model but the magnitudes were much smaller than expected and the distribution did not show the expected pattern. This could be the result of a more stable body-centered reference point on the back vs. the front of the body. The spine provides a strong tactile landmark on the back of the body; one participant spontaneously reported that he felt he could “feel” his backbone during the task, supporting this idea. Further, the research demonstrating a misperception of the orientation of the body is usually conducted by asking participants to make judgments regarding spatial locations relative to their body-straight-ahead (Harris & Smith, 2008; Hill, 1972; Morgan, 1978; Yamaguchi & Kaneko, 2007). Analogous research investigating effects on the body-straight-behind are rare, especially as visual probes are often used. One study, using auditory probes presented from behind (Lewald & Ehrenstein, 2001), indicated that auditory localization is affected in the same direction (that is, gazing to the left is associated with perceiving sounds further to the right in both front and rear space) and by similar magnitudes when presented from the front or back. If touch location were indeed coded in a body-centered reference frame during the static task, it would imply that the perceived "body-straight-behind" was less affected by gaze displacement than the perceived body-straight-ahead. If the body-straight-behind were more stable (perhaps as a result of the spine reference point) that might explain why perceived touch locations were less affected by gaze displacement. We therefore suggest that in the static task, touch locations on the back may be coded in a body-centered reference frame as they are on the front, but with reference to the backbone rather than to the body-straight-ahead.

Dynamic task

In the dynamic task we expected errors to be associated with the perceived direction of gaze (Figure 4.1A and B). The magnitude of effect (approx. 1.6 cm on the front and back) and the observation that it only occurred on the side of the body to which gaze was directed are consistent with predictions based on touch being referenced to the perceived gaze direction. However, the direction of the effect was in the opposite direction to that predicted: instead of rightward gaze displacement being associated with clockwise displacement of perceived touch location, it was associated with counter-clockwise displacement and visa versa for leftward gaze displacement (Figure 4.4D). One possible explanation for this is that during this task, touch locations were coded not in a gaze-centered reference frame but instead in a body-centered reference frame. It makes sense that invisible parts of the body may not be coded in a gaze-centered system. However, if touch location on the back were coded in a body-centered frame even during the dynamic task, what then could explain the obvious differences between the static (Figure 4.3D) and dynamic (Figure 4.4D) data?

The flat body hypothesis

An alternative, bold hypothesis is that touch on the back may be perceived with reference to points on the front – through the body – and thus be liable to the same influences (and the same direction of displacement) as those on the front. In this model the body is not represented as a three dimensional solid object but is instead flattened with the front and back being treated equivalently. This hypothesis is illustrated in Figure 4.6. This strategy might be encouraged by our recording method which required participants to project the back of their bodies through the body onto the response line presented in front of them. The flat body hypothesis is conceivable considering how the body representation is built up and maintained. The tactile component of the body representation is composed of a collection of flat skin maps (Longo & Haggard, 2012). The somatosensory cortex represents the body surface, but the spatial layout of the skin surface (size and shape) is lost. A novel representation of the size, shape and positioning of the body must be created centrally in order to locate the touch in space. How might this folding of the flat skin maps be achieved? If there were a "pinning" or "alignment" of the representation of the back onto the front then this might represent a basis for touches on the back being displaced in lock-step with those on the front.

Other evidence has emerged that supports this special relationship between the front and back. Vibration applied to the back of the body can mask a touch on the front of the body, but only when they are aligned "through the body" (D'Amour & Harris, 2014). Similarly, when the letters "b", "d", "p", and "q" are drawn on the skin on the front of the body they are perceived as if the observer's locus is within the body (a "q" from the experimenter's perspective is perceived as a "p" by the participant). But when the same character is drawn on the back it is perceived as if it were the other way round (a "q" from the experimenter's perspective is perceived as a "q" by the subject). Though there is some variability in participants' responses, more than 70% of participants give responses consistent with the idea that tactile patterns are perceived as if observers had a flat body and were located outside and behind their body (Natsoulas & Dubanoski, 1964). That is, as if points on the back of the body were mapped through the body onto corresponding points on the front.

Although more evidence is required before accepting the flat body hypothesis, it could explain the differences between our results for the static and dynamic conditions and explain the startling similarity in the pattern and magnitude of the front (Figure 4.4B) and back (Figure 4.4D) data in the dynamic task.

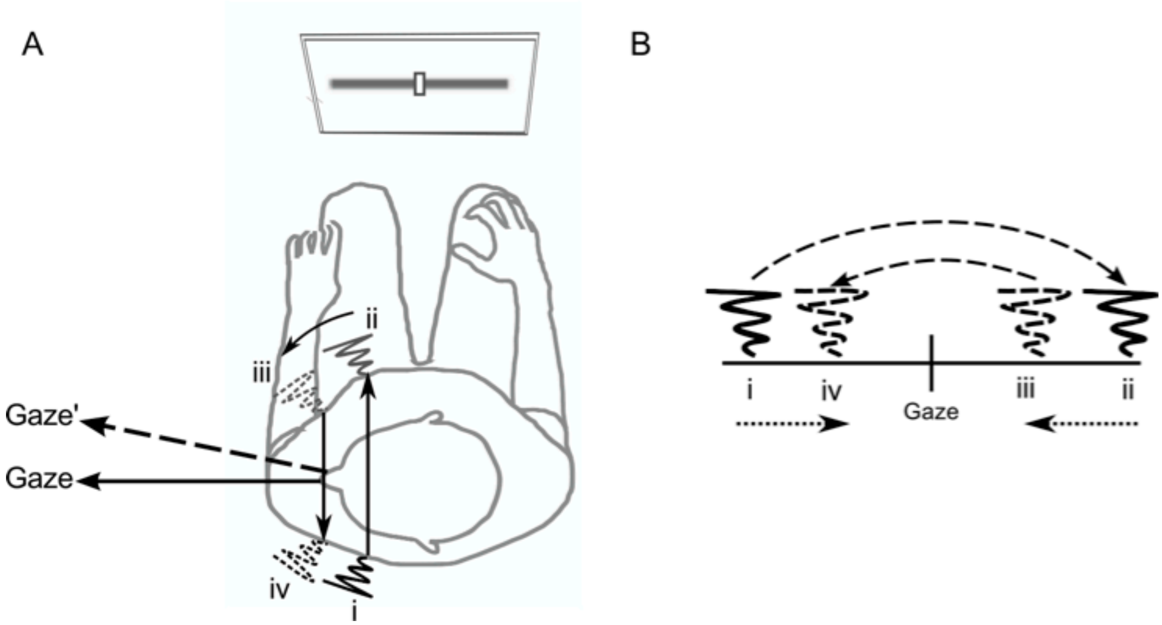

Figure 4.6. The flat body hypothesis. Illustration of how head orientation could affect localization of touch on the back by referring it to locations on the front. A: The tactile stimulus is applied to the back (i) while the participant's head is oriented eccentrically on the body. The location on the back is then referred to a location on the front (ii). Next, that location is compared to an underestimated representation of gaze, resulting in coding the location as closer to the gaze direction (iii). That location is then referred back to the back (iv). B illustrates all the localization shifts described in a gaze-centered reference frame.

Why is the effect asymmetric on the left and right of the body?

During the dynamic task for both the front and back only the touches on the side of the body to which the head was turned were affected by eccentric gaze position. We hypothesize that this asymmetry may result from combining visual and somatotopic body representations. In visual terms, the body may be divided into an area within the visual field and an area outside this zone. In somatotopic terms, primary somatosensory maps represent the body in fragments of distinct skin regions divided by anatomical landmarks such as joints and the navel (Cholewiak et al., 2004; Cholewiak & Collins, 2003). We postulate that when gaze is oriented 90° to one side, only the somatotopic representation within the visual field is put in register with the gaze or body reference frame. This would be another example of vision of the body modulating how touch is coded (c.f., Botvinick & Cohen, 1998; Kennett, Taylor-Clarke, & Haggard, 2001; Ramachandran & Rogers-Ramachandran, 1996) although it is important to point out that, even with the head at around 90°, the lower back cannot actually be seen because it is occluded by the shoulder. However, under our flat body theory the back is projected onto the visible front so not being able to see the lower back would not matter. Perhaps turning the head to one side primes touches on that side to be transformed into a reference frame related to action (i.e. a gaze-centered, see Colby, 1998; Mueller & Fiehler, 2014).

Conclusions

We conclude from these results, together with other results from the torso and arm reviewed above, that coding of the location of a touch can be in different reference systems depending on the task and that touches on the back are subject to the same transformations. Experiments of this type provide us with important clues about the nature of the body's representation in the brain.

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Chapter 5. Is Touch Localization Shifted By or Attracted Towards Gaze Position?

Abstract

We have previously shown that perceived location of touch on the torso is affected by gaze position. We suggested a model based on the idea of an underestimated gaze signal that could explain why touch localization is shifted in opposite directions by gaze depending on whether touch is coded relative to the orientation of gaze or of the body. This model predicted that all touches coded in one reference frame would shift by an amount proportional to gaze eccentricity (errors would be a function of gaze). Here, an alternative model is considered where gaze position acts as an attractor for the perceived position of a touch (errors would be a function of the difference between gaze and touch). Nine participants reported the perceived locations of eight vibrotactile stimuli arranged across the front of the torso. Vibrations were delivered while gaze was directed at one of seven locations between ±45°. Before reporting perceived location, participants returned their gaze to center. Three response methods were used: a visual method (reporting the location on a line), a numerical method (reporting a number for the part of skin stimulated), and a motor method (pointing to the perceived location). For the visual response method, gaze related errors were better described as a function of the difference between gaze and touch than as a function of gaze. This indicates that, at least with a visual response method, touch locations are attracted towards the location of gaze rather than shifted in the direction of gaze, indicating that effect is

not a result of an underestimated gaze signal. When response was made by pointing there was no effect of gaze direction, indicating that a gaze-independent reference frame was used. When the numerical response method was used errors were not well described as either shifted by or attracted towards gaze. These results indicate that reference frames for touch localization depend on the type of response required to be made.

Introduction

The perceived location of touch is affected by gaze position. This effect has been taken to indicate that gaze is a reference point for touch localization (Harrar & Harris, 2009, 2010; Pritchett, Carnevale, & Harris, 2012; Pritchett & Harris, 2011). We have proposed that gaze-related errors in localization could be caused by an underestimated representation of gaze, which is then used as a reference point for touch localization (Pritchett et al., 2012). Figure 5.1A shows how an underestimated representation of a gaze reference point would affect touch locations coded in that reference frame. When gaze is clockwise on the body all touch locations would be *shifted in the same direction* around the body, this will be referred to as the shifter model. Here we test this model versus an alternative which proposes that touch locations are perceived as closer to gaze than they actually are, this alternative is referred to as the attractor model, illustrated in Figure 5.1B.

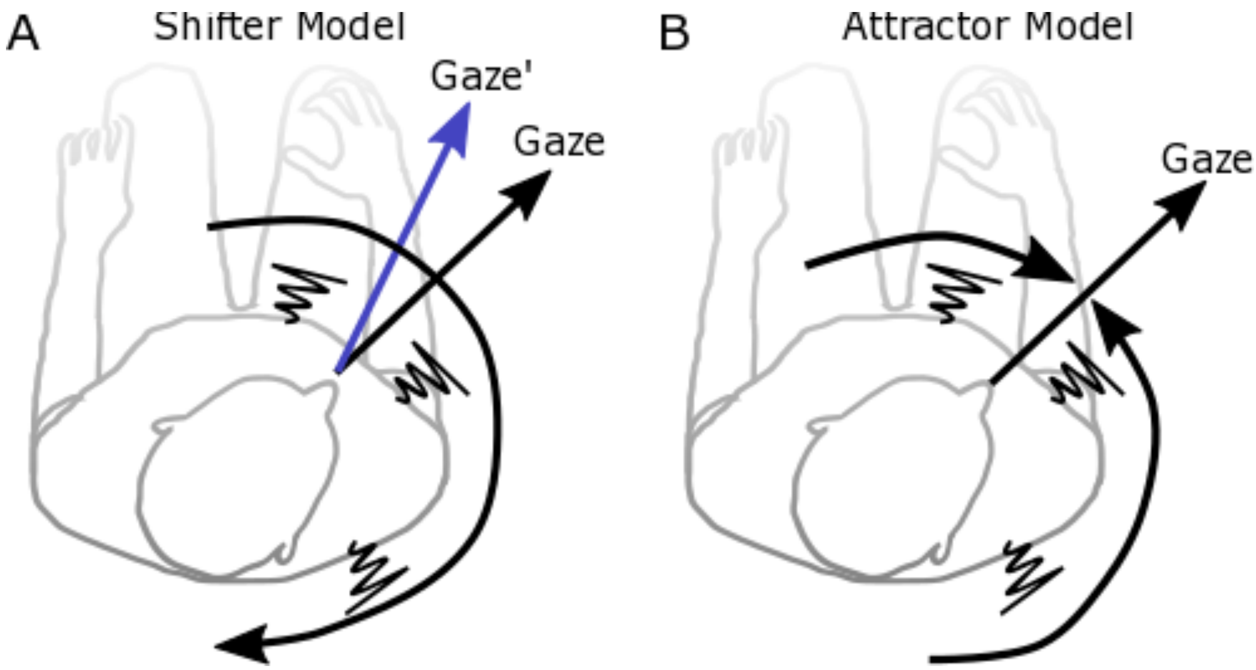

Figure 5.1. Two illustrations of how gaze could affect the coding of touch localization. A: "Shifter model": A neural signal of gaze angle is underestimated, if used as a reference point for touch localization, all touches would be perceived as shifted in the same direction around. B: "Attractor Model": If touch locations were attracted towards the location of gaze touches on either side of gaze would be shifted in opposite directions relative to the actual location of the touch.

The shifter model was useful for explaining why gaze affects touch locations in opposite directions depending on the experimental task (Pritchett et al., 2012). During a dynamic task where gaze was oriented to either the left, right, or center, and then reoriented to the center on every trial, touch localizations were shifted in the same direction as gaze. During a static task, where the body and gaze remained at the same orientation throughout all trials, touch localizations were shifted in the direction opposite to gaze. We argued that these effects suggested that touch location is coded using different reference frames depending on the task. An underestimated representation of gaze angle can also affect the perceived direction of straight-ahead (Hill, 1972; Morgan, 1978; Yamaguchi & Kaneko, 2007), which, if used as a reference point, would cause shifts in the opposite direction of gaze. We therefore concluded that touch localizations shifts in the direction opposite to gaze indicated body-centered coding, and shifts in the direction of gaze indicated gaze-centered coding. Mueller and Fiehler (2014) also demonstrated that having an effector (arm or gaze) move between touch and response caused a switch from body to gaze-centered reference frames.

In the current chapter the dynamic task will be used, that means that there will be an effector movement (gaze shift from an eccentric position to the center) in between each touch presentation and localization response. As already described, we expect the dynamic task to cause localization errors either in the direction of (shifter model), or towards (attractor model) the angle of gaze at the time of touch presentation. In either case we predict positive slopes for localization error plotted as a function of gaze. This experiment does not also include a static task equivalent to Experiment 2 in Pritchett et al. (2012) (Chapter 2), which was found to cause gaze-related errors in the opposite direction of gaze. Errors in the opposite direction of gaze would not be compatible with the attractor model where touch location is expected to be shifted towards gaze, though it could be compatible with an attracted-toward perceived body-midline model. As described in Chapter 3, the opposite-of-gaze effects in the static task are compatible with coding touch locations relative to a misperceived angle of the body-straight ahead (analogous to the shifter model). In Chapter 4 where touches were applied to the back we found only a very small effect of gaze in the static task, it is therefore only the dynamic task where we are puzzling over whether tactile localization is shifted in the direction of gaze (shifter model) or toward gaze (attractor model). Therefore in this chapter only the dynamic task will be used.

The shifter model is consistent with effects of gaze on touch locations on the arms and on the front of the body (Harrar & Harris, 2009, 2010; Harrar, Pritchett, & Harris, 2013; Pritchett et al., 2012; Pritchett & Harris, 2011). However, when we applied touch locations to the back of the body in the dynamic (i.e. gaze related) task, effects were not consistent with this model (see Chapter 4). When the head was oriented clockwise on the body, errors during the dynamic task were in a counter-clockwise direction on the back. This suggests that either touch locations on the back of the body are coded differently than those on the front (perhaps locations on the back are referred to locations on the front, as described in previous chapter), or that the proposed mechanism (that touches are coded relative to an underestimated gaze signal) causing the effect is not correct. Instead, it could be that touch locations are attracted towards the location of gaze.

Previous research on effects of gaze direction on tactile localization has not specifically considered whether effects are better described as a shift in the direction of gaze or as an attraction towards gaze. However, research on effects of gaze on visual localization has considered this. Hill (1972) showed that when the eyes are eccentric in the head, visual stimuli are mislocalized in the opposite direction of gaze direction. He examined whether the effect was a result of an underestimate in the neural signal for eye position (similar to the shifter model), or as a result of underestimated retinal sign information (similar to the attractor model). He had participants turn their head towards visual targets that were presented either foveally to assess perceived eye position, or peripherally to assess retinal sign information. Results indicated that eye position was underestimated while retinal localization was not systematically affected. However, in a follow up study using similar procedures Morgan (1978) found that both perceived eye position and retinal sign information played a roll. More recently, Bock (1986) and Henriques, Klier, Smith, Lowy, and Crawford (1998) found that only retinal sign and not gaze angle affected visual localization. Recent behavioral (Harrar & Harris, 2009, 2010; Harrar et al., 2013; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012; Pritchett & Harris, 2011) and neurological (Badde, Röder, & Heed, 2014; Forster & Eimer, 2005; Gherri & Forster, 2014; Heed & Röder, 2010; Ley, Steinberg, Hanganu-Opatz, & Röder, 2015) research has suggested that tactile stimuli may be coded in a visual reference frame. If this is true, then the same mechanisms that cause localization errors in vision may also cause errors for tactile stimuli.

The most intuitive difference between the attractor and shifter models is, as already described and illustrated in figure 5.1, that the shifter model predicts gaze related errors in the same direction regardless of the location of the touch, while the attractor model predicts errors in opposite directions depending on the location of the touch relative to gaze. If gaze-related errors occurred in isolation we could therefore look for a sign-change in error for touches on either side of the gaze angle. However, there are other factors affecting accuracy of touch localization. For example, previous research has shown consistent localization errors toward the navel for touches to the torso (Cholewiak, Brill, & Schwab, 2004). It will be impossible to detect a sign change in localization error around the angle of gaze if in addition to gaze-related errors there are other body-position related localization errors such as this, especially if they are larger than the gaze-related effects. Thus, instead of trying to detect a sign-change around the angle of gaze I will turn to another more useful difference in the predictions generated by the shifter and attractor models: the shifter model predicts that error will be a function of the angle of gaze while the attractor model predicts that error will be a function of the difference between the angle of gaze and the angular location of the touch on the body. Even if there are other factors that affect localization, the correct model (shifter or attractor) should explain more variance in localization errors than the other. These models will now be described in more detail.

Under the shifter model, all touch locations would be shifted in the same direction as gaze, by an amount proportional to the angle of gaze. This model predicts that when gaze is straight-ahead on the body (0-degrees) there would be no errors. This model predicts error would be a function of gaze:

$$E = g * b \qquad \text{(Eq. 1, shifter model)}$$

Where E is localization error, g is gaze angle, and b is a gain factor for the amount gaze is underestimated.

The attractor model predicts that touch locations would be attracted towards the location of gaze. Thus what matters here is the location of the touch relative to the location of gaze. Error would be a function of the difference between the location of gaze and of the location of the touch:

$$E = (g - t) * b \qquad \text{(Eq. 2, attractor model)}$$

Where t is a touch angle, and other symbols are as in equation 1.

This model predicts that touch localization would be accurate when gaze is at the same angle as touch on the body. The goal of the current paper is to determine whether error is better explained as a function of gaze (the shifter model) or as a function of gaze minus-touch (the attractor model).

Previous research has suggested that gaze has a linear effect on errors. That is, the shift is proportional to the angle of gaze. This is reflected in my linear equations 1 and 2 for the two models. However, most previous research has only used a few gaze locations so it is difficult to determine whether the function is in fact nonlinear. When five gaze locations were used by Pritchett and Harris (2011) the results did suggest a nonlinearity where effects asymptote by 30 degrees (that is, effects were proportional up until around 30 degrees and then did not increase between 30 and 45 degrees), but results were not conclusive because only 5 gaze locations were used. Additionally no study, to date, has used both a large number (>4) of gaze locations and a large number of touch locations (>4), which is required to conclusively determine whether error is in fact a function of gaze or of the difference between gaze and touch (Harrar & Harris, 2009, 2010; Harrar et al., 2013 used four gaze locations and four touch locations, Pritchett & Harris, 2011 used five gaze locations and two touch locations, Pritchett et al., 2012 used three gaze locations and eight touch locations). The current study used seven gaze locations (from -45 to +45 degrees) and eight touch locations (all on the front of the torso, approximately -60 to +60 degrees) allowing for a better test of whether effects of gaze are a function of gaze (shifter model) or a function of the difference between gaze and touch (attractor model) and whether the effect is linear.

Shifter Models

Figure 5.2 shows the predictions of a linear shifter model (error as a function of gaze) plotted as a function of gaze, touch, and gaze-minus-touch. In this model, only gaze location affects the perceived location of touch (2A); the location of touch on the body has no effect on the direction of errors (2B). Plot 2C shows that gaze minus-touch would still explain some variance in errors (because gaze and gaze minus touch are correlated), but would explain less than gaze alone.

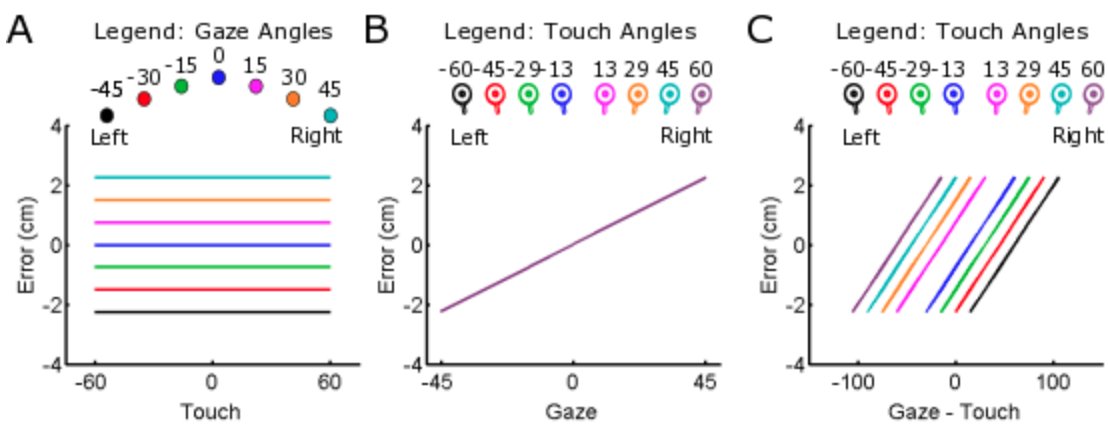

Figure 5.2. Predictions of the shifter model. A: Location of touch does not affect errors. B: Errors are a function of gaze. C: The difference between gaze and touch explains some error, but less than gaze alone. Different colored lines represent the errors for particular gaze angles in A and for particular touch locations in C as shown in the legends above the graphs.

Under this theory, touch location would not be predicted to have any effect on errors: that is the error for all touch sites are the same for a given gaze angle. This prediction is probably not correct, because, as described above, there are other things that influence accuracy of touch localization. Touches closer to body landmarks are known to be localized more accurately and touch locations are generally perceived as closer to body landmarks than they actually are (Cholewiak et al., 2004; Cholewiak & Collins, 2003). Therefore, we may predict that errors will be smaller for touches close to the navel (since all touches in the present experiment are along the front of the torso), touches on the left of the body will have errors to the right, and errors to the right of the body will have errors to the left, this can be modeled as a negative-sloped linear function of touch location with the navel is coded as 0 on the body and locations on the left coded as negative. When combined with the shifter model, this provides the combined *shifter-plus* model (plotted in Figure 5.3):

$$E = g * b_1 + t * b_2 \qquad \text{(Eq. 3, shifter-plus model)}$$

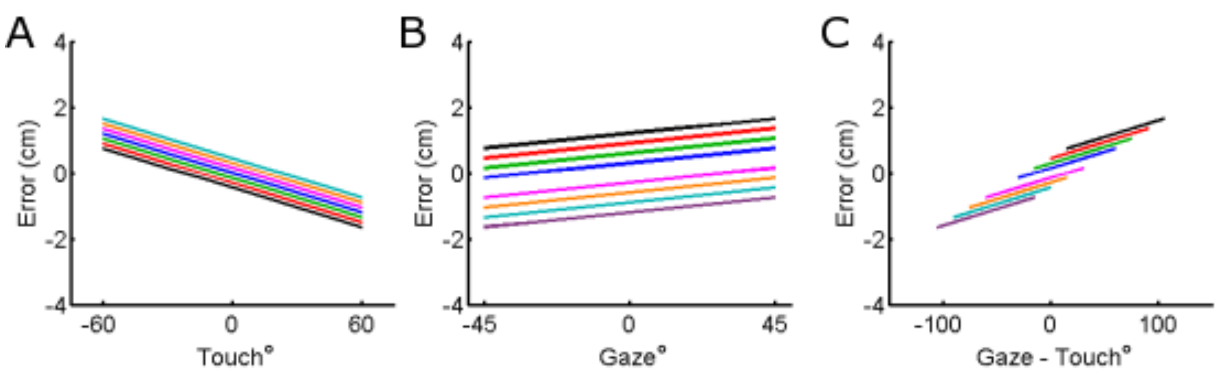

Figure 5.3. Predictions of the shifter-plus model, where gaze and touch have independent linear effects. Format and legend as in Figure 5.2.

Attractor Models

Figure 5.4 shows predictions of a linear attractor model (localization error as a function of gaze-touch) plotted as a function of gaze, touch, and gaze-minus-touch.

Plot 4C shows that errors would be well explained by the difference between gaze and touch angle. Plots 4A and 4B show that both gaze and touch location would also predict errors. In fact, under this model gaze and touch would have equal and opposite effects:

$$E = (g - t) * b \qquad \text{(Eq. 2)}$$

by the distributive property:

$$E = g * b - t * b \qquad \text{(Eq. 4, rewritten attractor model)}$$

This linear version of the attractor model turns out be just a special case of the shifter-plus model.

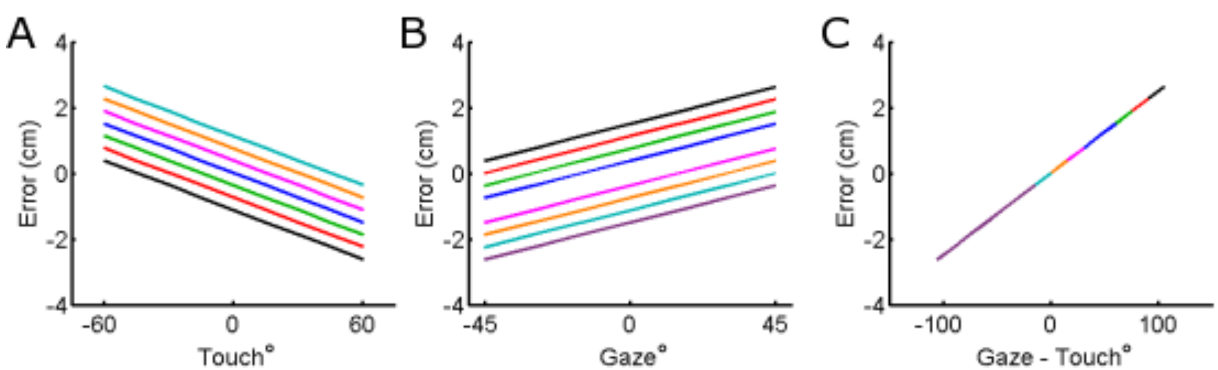

Figure 5.4. Predictions of the attractor model. A and B: Both touch and gaze have equal and opposite linear effects. C: The difference between gaze and touch explains error in localization. Format and legend as Figure 5.2.

Luckily, the attractor model is unlikely to be linear as that would suggest that touches very far from the location of gaze would be attracted towards gaze the most. Instead, we predict that there will be a region around gaze where touch locations are attracted more, and that the strength of attraction will diminish with the distance between gaze and touch angle. We model this as a normal distribution centered at the location of gaze:

$$E = (g - t) * b * N(g - t, 0, \sigma) \qquad \text{(Eq. 5, nonlinear attractor model)}$$

where $N(g - t, 0, \sigma)$ is a Gaussian normal probability distribution centered at the location of gaze with width of σ. This will be called the Gaussian-pull attractor model. Note that the strength of the pull may not necessarily follow a Gaussian distribution: it could be exponential or another function. To determine which of many functions the pull strength follows would require finer resolution of touch and gaze locations and is beyond the scope of this analysis. Here, the Gaussian function is arbitrary; the important point is that we predict the pull strength will diminish as touches become further away from gaze. Figure 5.5 shows the predictions of this model, plotted as a function of gaze, touch, and the difference of gaze and touch.

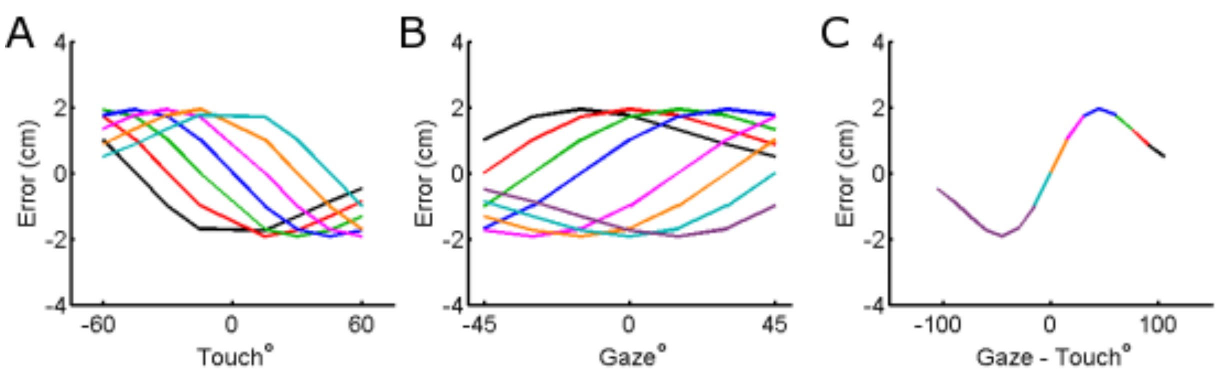

Figure 5.5. Predictions of the Gaussian-pull attractor model. A and B: both touch and gaze have equal and opposite non-linear effects on localization. C: Errors are a function of the difference between gaze and touch location; effect is reduced when touch location is far from gaze location. Format and legend as Figure 5.2

Impact of Response Methods

A final purpose of the research described here is to examine the impact of response method on the gaze-related touch localization errors. A strength of the doctoral dissertation by Harrar (2010) was the demonstration that touch localization is affected by gaze regardless of whether response was made using visual comparison (Harrar and Harris 2009), pointing (Harrar and Harris 2010), or a method called the Segmented Space Method (SSM), which we believed to require no visual component (Harrar et al., 2013). In the SSM, participants are asked to imagine dividing a spatial region into a number of segments and give each of those segments a number. Then they report localization estimates by simply reporting the number of the segment rather than by making a visual comparison or motor response to that location.

Although Harrar found significant effects of gaze all in the same direction as gaze in all of these response methods, each experiment was performed at different times with different participants. Here I will use three different response methods, a visual scale (as used in Chapter 3 and 4), a pointing response, and the SSM. Since the visual scale explicitly requires representing location visually, it is most likely to show an effect of gaze direction. In contrast, for the pointing response the location can be kept in an entirely body-related representation, so gaze location is less likely to have an effect there. The SSM task is intermediate between these two, neither requiring a visual or body-based representation for response. Each of these will be conducted with the same set of participants with response method order counterbalanced between participants. This will allow for direct comparisons between the different response methods.

Method

Participants

Nine participants (4 male, 5 female) between the ages of 20 and 30 completed all three experiments. All participants reported having normal sense of touch and vision, and all were right handed. All participants gave informed consent prior to participation and the York University Ethics board approved all procedures.

Apparatus

Tactile stimuli. An array of eight vibrating tactors (Model C2, Engineering Acoustics, Florida USA) was used to deliver tactile stimuli. The vibration stimulus was an amplified 250 Hz, 50 ms sine wave. Intensity was randomly chosen from 5, 6.7, 8.3, or 10% of maximum possible intensity so that participants could not memorize subtle differences between tactors. Stimuli were suprathreshold and easily perceptible. To mask the noise made by the tactors, a loud auditory signal composed of a 250 Hz signal and pink noise was continuously played through loud speakers during the experimental procedure. Tactors were mounted on a belt and worn around the participants' body. The array was worn centered around, and just above the navel. The tactors were at 4, 8, 12 and 16 cm on either side of the navel (see Figure 5.6).

Gaze manipulation and recording. A set of 7 LEDs were used as gaze targets, they were placed at 0, 15, 30 and 45 degrees to the left and right of the participant's straight-ahead. Figure 5.7 illustrates the relative positions of LEDs, tactors and the participant. Eye and head angle were measured using a head-mounted gaze tracker which is accurate within one degree (3D workspace, Arrington Research, Arizona USA).

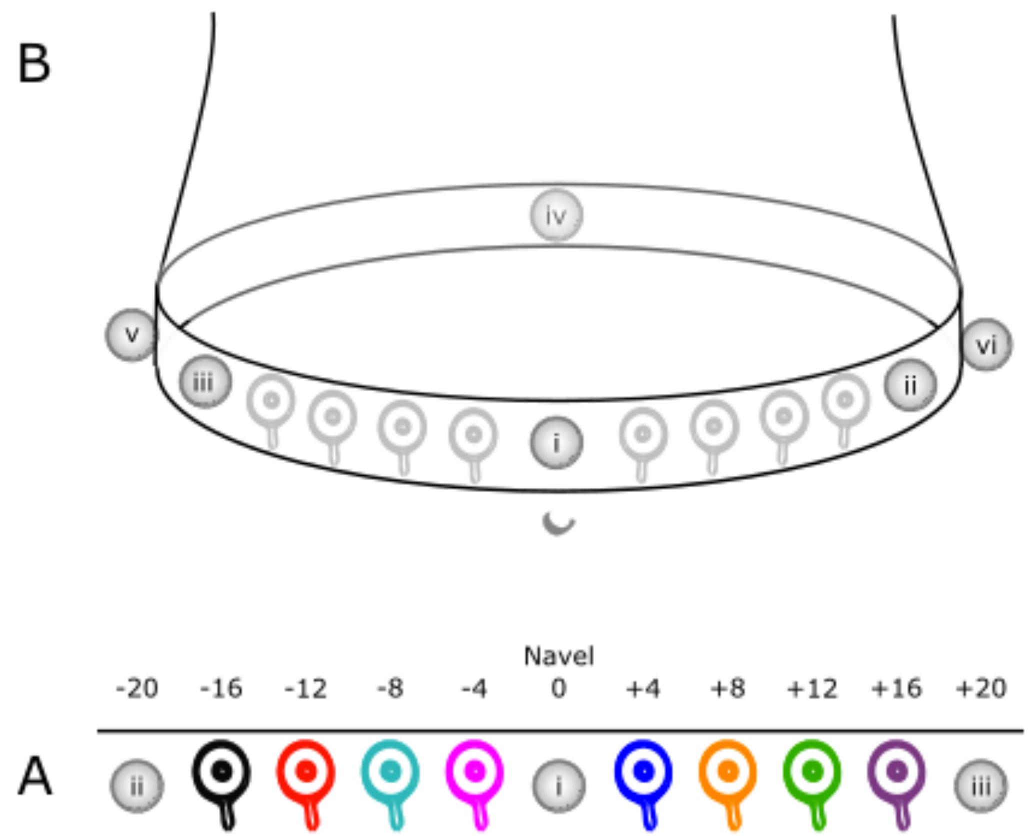

Figure 5.6. Arrangement of tactors and reflective markers on a belt worn around the participant's torso. A: Locations of each of the 8 tactors relative to three of the reflective markers. Reflective marker *i* was aligned with the participant's navel. The tactors were positioned at 4, 8, 12, and 16 cm on either side of that reflector and the navel. Markers *ii* and *iii* were placed at 20 cm from marker *i.* B: arrangement of the tactors and reflective markers around the body. Marker *iv* was placed on the participant's backbone. Markers *v* and *vi* were placed at locations indicated by the participant to be at 90-degrees to their left and right.

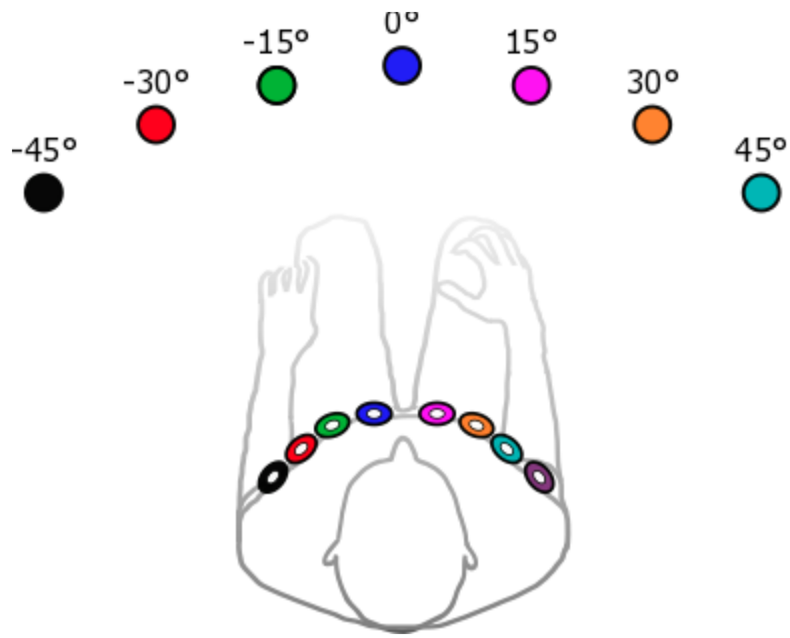

Figure 5.7. Illustration of relative positions of LEDs (solid circles) and tactors (open ellipses near illustration of the body). Colors correspond to the color codes used in figures 5.2-5.5 and 5.9-5.20.

Body and point recording. Body size, location, and orientation were recorded using a motion-capture system (Flex 3 OptiTrack, Natural Point Inc., Oregon USA), which uses infrared emitting and detecting cameras to track locations of rigid bodies with reflective markers affixed. Reflective markers were placed on the head-mounted gaze tracker to record the location and orientation of the head. Also, six markers were placed on the same belt that held the tactile array (see Figure 5.6). One marker (i in Figure 5.6) was placed in the middle of the array and was used by the participant to center the array on their body. Two markers (ii and iii in Figure 5.6) were placed at 4 cm beyond the final tactor on either end the array (20 cm from the center). The fourth marker (iv in Figure 5.6) was on the participant's spine. The final two markers (v and vi in Figure 5.6) were placed at the location participants reported to be 90 degrees to their left and right. These markers were used to record the location and orientation of the participant's' body. They were also used to estimate the angle of each tactor on each individual's body, which differed between participants due to individual differences in body size and shape (details on how angle were determined for each participant based on these body markers is explained under data analysis)

For the pointing response, a plastic pointer with reflective motion tracker markers affixed (supplied by Arrington Research in the 3D Workspace) was used. A button was attached to the pointer that participants pressed to trigger the computer to record the location of the marker at the end of the pointer (see Figure 5.8c). During pilot testing, we found that when the pointer was close to the markers on the body accurate pointing locations were not always recorded. Therefore, for the pointing response experiment, all the markers on the tactile array were removed, and instead five markers were placed on a second belt that was worn higher on the participant's body. These markers still allowed us to determine the location of the pointer relative to the body, and the location and orientation of the participant's body.

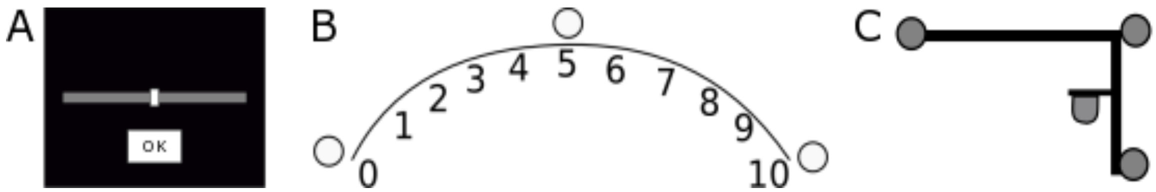

Figure 5.8. Three response methods used in separate counterbalanced experiments. A: A visual line displayed on a screen represents the extent of the tactile array, with line ends anchored to the markers placed 4cm beyond the final tactor on the array. B: A visual aid provided to participants to assist in numerical reports. Numbers 0 and 10 were anchored to the markers 4cm beyond the final tactor. Number 5 was anchored to the marker placed at the navel. C: The pointing device provided by Arrington Research with reflective markers and a button attached. Participants placed the marker at the tip of the pointing device along the tactile array at the location at which the touch was perceived.

Procedure

Setup. Participants were initially setup in the apparatus by attaching the tactor belt, which already had all of the tactors and three of the reflective markers (markers i, ii, and iii in Figure 5.6 indicating the center and 4 cms beyond the ends of the tactile array) affixed. The belt was adjusted such that the marker indicating the center of the array was just above the navel. Participants were instructed that the other two markers (ii and iii in Figure 5.6) represented the extent of the tactile array. A fourth marker was then placed on the belt at the participants' spine (marker iv in Figure 5.6). The participant was then asked to point (using their finger) at the locations of their body that represented 90 degrees to their left and right. Typically the locations indicated corresponded to a seam on their clothing. The final markers (v and vi and Figure 5.6) were placed at those locations.

Next the participant placed the head-free gaze tracker onto their head, and the experimenter adjusted the head-mounted cameras so that they pointed at the eyes using the video that the cameras generated. Three rigid bodies were then defined corresponding to the participant's head, body and the pointer (i.e. markers representing the participant's, head, body and pointer were clustered indicating that the distances between markers for each cluster were constant) in the motion tracking system.

Calibration. The gaze tracking calibration procedure in 3D workspace supplied by Arrington Research was then conducted. This procedure involved calibrating the head and eyes relative to a visual display fixed directly in front of the participant. Once that procedure was completed a separate gaze calibration and validation procedure relative to the LEDs was conducted in MATLAB. Following that calibration the experimental procedure commenced.

Experimental procedure. On each trial a randomly selected LED was lit and participants made a natural gaze shift to look at the LED. Gaze was monitored until both the head and eyes orientation stabilized and gaze was within 7 degrees of the LED. The tactile stimulus was then delivered via a randomly selected tactor on the array. Next, the LED straight ahead of the participants was lit, and participants shifted their gaze toward that LED, while gaze was continuously monitored. Once their gaze was stabilized within 7 degrees of the central LED the participant was prompted for response. Three response methods were used in separate counterbalanced experiments completed on separate days, which will be described next. Every combination of 7 LEDs and 8 tactors was presented 8 times for each participant in each response method. After each set of 56 trials was completed participants were informed using a message on the display that they had completed one-eighth of the experiment. They were encouraged to take a brief break, but did not stand or leave the apparatus until all of the trials were completed.

Visual-line response. The visual-line response method used a long horizontal bar displayed on the screen with a slider (see Figure 5.8A). Participants were instructed that the bar represented the length of the tactile array, with the ends of the line representing the locations of the reflective markers placed off the ends of the tactile array. They used a slider to indicate the perceived location of a touch. Initially, the slider was placed directly in the middle of the horizontal bar. Participants adjusted the slider by using the computer mouse (used with the right hand) and either clicking on the location they wished to report or by dragging the slider to that point. Once they were content with the report they clicked an "OK" button on the screen, triggering the beginning of the next trial. Since the ends of the line represented locations 20 cm from the navel, and the tactors were placed at 4, 8, 12, and 16 cm from the navel, the accurate locations of tactors were 0.1, 0.2, 0.3, 0.4, 0.6, 0.7, 0.8 and 0.9 proportions on the line. This response method is similar to that used in previous research (Ho & Spence, 2007; Pritchett et al., 2012), except that the ends of the line were anchored to locations 4 cm beyond the final tactors on the array, rather than to the final tactors themselves.

Segmented space method. In this method participants were asked to divide up a region of space and assign numbers to different regions. They then report a number that indicates the perceived location of a touch. Participants were instructed that the locations of the markers placed off the ends of the tactor array would be represented by numbers 0 (the marker to the left of the midline), and the number 10 (the marker on the right), the number 5 represented a location in the middle of the body, just above the navel. Participants viewed the image shown in Figure 5.8B while responding to assist them in determining the number to report. The accurate responses for the tactors were thus 1, 2, 3, 4, 6, 7, 8, and 9. Participants entered their response using a keyboard. They were free to report any number, including decimals or numbers outside of the range 0 to 10, though numbers outside that range were never used. Participants could use the backspace on the keyboard to make corrections. Once a number was entered participants hit the enter key, triggering the next trial. This response method is similar to that used by Harrar et al. (2013).

Pointing response. For the pointing response participants used the pointer supplied by Arrington Research that has reflective markers attached allowing tracking by the motion-capture system (see Figure 5.8C). Participants held the pointer in their right hand and rested that hand on a table approximately 20cm in front of them in the beginning of each trial and while touch stimuli was applied. After the touch was applied and gaze was subsequently centered, participants used the pointer to indicate the location of the touch. They placed the end-point of the pointer along the tactor belt at the location they perceived the touch, and then pushed the button attached to the pointer. If the pointer location was determined by the motion-tracking cameras a message appeared on the screen "Point Recorded" prompting the participant to return their hand to the starting location, resting on the table in front of them. If the location of the pointer could not be determined (due to markers being blocked from the cameras' view) a message on the screen reported that "Pointer Not Visible", participants then adjusted the orientation of the pointer, keeping the end point at the same location, until the location was successfully recorded, this recording error occurred on 24% of trials, and was more likely to occur for touch locations on the left end of the array. The system records the location of the pointer in room coordinates. To determine the location of the pointer relative to the body, the location and orientation of the body in room-coordinates was also recorded at the same time the pointer location was recorded. The next trial was triggered after the pointer and body locations were recorded and the pointer was returned to the starting location.

Data Analysis

The dependent variable in all analyses is the absolute error in touch localization. The "accurate" location was subtracted from each localization response. For the visual-line and SSM, responses are one dimensional between 0 and 1 (visual-line), and 0 and 10 (SSM), where 0 is the marker 4 cm off the left end of the array. Responses in the SSM were occasionally much larger than 10 (e.g., 70), probably due to mistakes in response input. Those responses were removed from the data set.

These numbers were converted to cm, using the fact that the extent of the tactile array was 40 cm.

For the pointing method, responses were recorded as xyz coordinates relative to the room. The locations of the body markers were also recorded (in room-coordinates) to estimate the size and shape of participants' bodies. As mentioned before, the body markers interfered with recording pointing responses so the body markers' locations were recorded before the experiment rather than continuously during the experiment. Instead, we recorded the location and orientation of the participant's body during the experiment by a different set of body markers worn higher on the participant's body, around the rib cage (not shown).

To convert the pointing data from room to body coordinates we first subtracted the location and orientation of the body at the time of response from the response data, accounting for any small movements of the body during the experiment. Any responses that were not along the tactile array were discarded. We transposed the response and body-marker data so that the navel was at the coordinate origin. To complete the conversion from room to body-coordinates, we then rotated the response and body-marker data so that the coordinate axes were aligned with the tactile array. Figure 5.8 shows the response and body marker data for one participant in body-coordinates. We then determined the actual locations of each tactor by fitting a circle to the responses and defining actual touch locations at 4, 8, 12, and 16 cm along the circumference of the circle from the navel. The coordinates of each response were also converted into an angle relative to the body straight ahead, and then to a distance in cm from the navel. This then allowed us to measure the difference between the actual tactor and the pointing response in cm along the tactile array.

The independent variables in the analysis were gaze angle and touch angle, and the difference between touch and gaze angle. Gaze angle was measured as the sum of eye and head angles using the gaze-tracking system. We defined zero gaze angle as straight-ahead looking at the central LED. Negative values indicate locations to the left of straight-ahead and positive values indicate locations to the right of straight-ahead. Touch angle was measured for each individual using the body-markers that were placed around the body (see Figure 5.9). The difference between gaze and touch was calculated by subtracting the touch angle from the gaze angle. Thus positive gaze-touch values indicated gaze was to the right of the touch and negative angles indicated gaze to the left of touch.

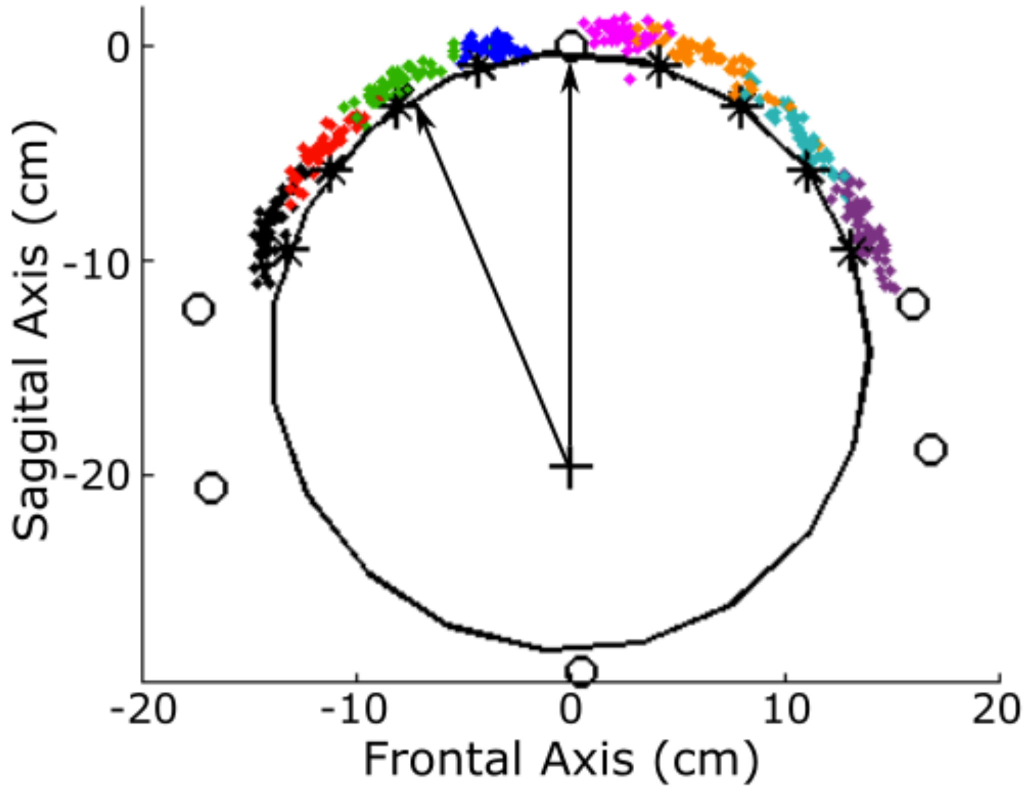

Figure 5.9. Pointing responses from one representative participant, in body-coordinates relative to the navel, are shown using small colored symbols (different colors represent pointing responses to different touch locations). Body markers are shown using the large black circles. Actual touch locations are shown using large black stars. The body origin (large + symbol) was defined as the point directly in-between the points perceived by the participant as 90-degrees to the left and right. We then defined a straight-ahead vector, from the body origin point to the navel, and a response vector from the body origin to the response point. We then defined the response in cm from the navel as the distance along the circle between the two vectors.

Results

The results from each response method were analyzed separately. In each case the analysis is intended to show whether the attractor or shifter models better predict the gaze-related tactile localization errors found.

Point Method

The localization errors from the pointing response method are shown in Figure 5.10. Errors are plotted as a function of touch, gaze, and gaze-touch. The effects of gaze and touch location were analyzed using a 2-way repeated measures ANOVA with gaze (7 locations) and touch (8 locations) as independent variables. There was no effect of touch location ($F(7,56) = 0.34$, $p = .69$), no main effect of gaze location ($F(6, 48) = 0.81$, $p = .55$) and no interaction ($F(42, 336) = 1.10$, $p = .37$). Since both the attractor and shifter models predict that there would be an effect of gaze location, neither model is supported by this data set, and further analysis to compare the models will not be reported.

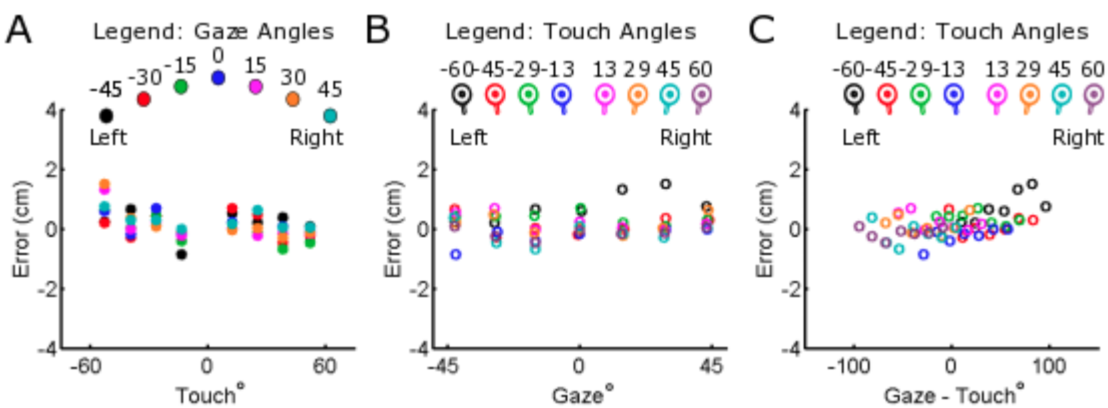

Figure 5.10. Localization error data from the Pointing response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Data is averaged results across 9 subjects. Colored filled circles in A represent localization error for different gaze locations, and colored open circles in B and C represent different touch locations.

Visual-Line Method

Localization errors from the visual-line method are shown in Figure 5.11. Errors are plotted as a function of touch, gaze, and gaze-touch. The effects of touch and gaze location were analyzed using a 2-way repeated measures ANOVA. There was a significant effect of touch location ($F(7,56) = 3.97$, $p = .046$), a significant effect of gaze location ($F(6,48) = 7.26$, $p < .001$), and a significant interaction of gaze and touch location ($F(42,336) = 4.37$, $p < .001$). The effect of touch location appears to be linear over this range (linear trend analysis $F(1,8) = 5.58$, $p = .046$): errors are to the right for touch locations on the left and vice versa, with touch locations near the navel having the smallest errors. This is consistent with perceiving touches as closer to the navel. The significant effect of gaze location indicates that gaze does affect the perceived location of touches. Both the attractor and shifter models predict this. The effect of gaze on touch localization errors does not appear to be linear, and is better explained as a cubic function (cubic trend analysis: $F(1,8) = 24.88$, $p = .001$) The interaction of gaze and touch suggests that the effect of gaze does depend on the location of touch, which is consistent with a nonlinear version of the attractor model but not the shifter model. To examine the interaction effect, simple effect one-way ANOVAs were conducted for each touch location separately. Results indicated that gaze location significantly affected touch locations furthest from the navel (touch location 1, 2, 3, 7, and 8, all $p < .005$) with non-significant (using Bonferroni corrected p-value of .006) effects at touch locations 4 ($p = .42$), 5 ($p = .043$), and 6 ($p = .027$). Regression analyses with Maximum Likelihood Estimates[3] (MLE) were used to examine whether the attractor or shifter model is a better fit for the data (see Table 5.1 for regression statistics).

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[3] MLE fits were performed using the mle function, part of the Stats4 package in the software R. MLE fits were made to data averaged across the 9 participants.

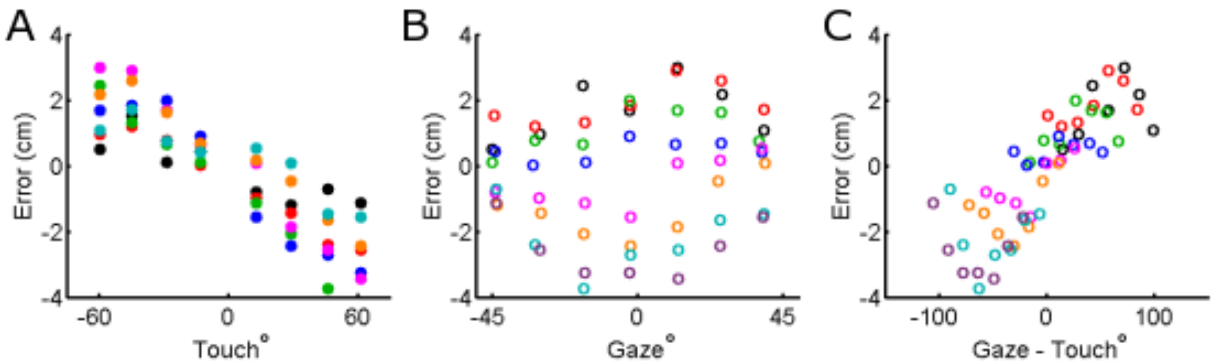

Figure 5.11. Localization error data from the visual-line response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Table 5.1.
MLE Regression Statistics for Visual Line Data

Model Name	Eq. Num.	Par 1	MLE (Std Err)	Par 2	MLE (Std Err)	R^2	RMSE	AIC
Shifter Models								
Shifter	1	*bg*	0.0095 (.008)			0.02	1.75	225.87
Shifter-Plus	3	*bg*	0.0098 (.004)	*bt*	-0.0388 (.0024)	0.83	0.73	130.20
Attractor Models								
Attractor	2	*bgt*	0.0296 (.003)			0.68	1.00	162.59
Nonlinear Attractor	5	*bgt*	8.7266 (.646)	*SD*	64.69 (7.46)	0.78	0.84	145.91
Modified Nonlinear Attractor	6	*bgt*	0.2136 (.012)	*SD*	53.77 (3.18)	0.86	0.66	118.82

Shifter models. The shifter model predicts that error will be a function of gaze location. In a linear regression, gaze only accounted for 2% of the variance in localization error (the proportion of variance accounted for comes from the coefficient of determination, R^2). An independent linear effect of touch accounted for 81% of the variance in error. A combined model (shifter-plus) including independent linear effects of gaze and of touch accounts for 83% of the variance in error (see Figure 5.12).

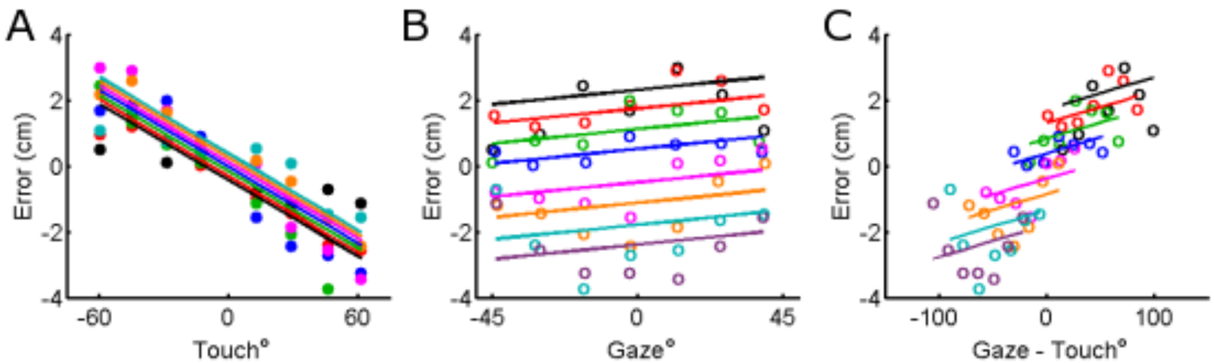

Figure 5.12. Shifter-plus model fit to the localization error data from the visual-line response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Attractor models. The attractor model predicts that error will be a function of the difference between gaze and touch location. Visual inspection of Figure 5.11C shows that error does indeed appear to be a function of the difference between gaze and touch, visual inspection also suggests that the function may not be linear as it appears rather S-shaped, especially for touch locations (shown in different colors) further from the navel. In a linear regression gaze-touch accounted for 68% of the variance in localization error. The Gaussian-pull attractor model accounted for 78% of variance in errors, (see Figure 5.13).

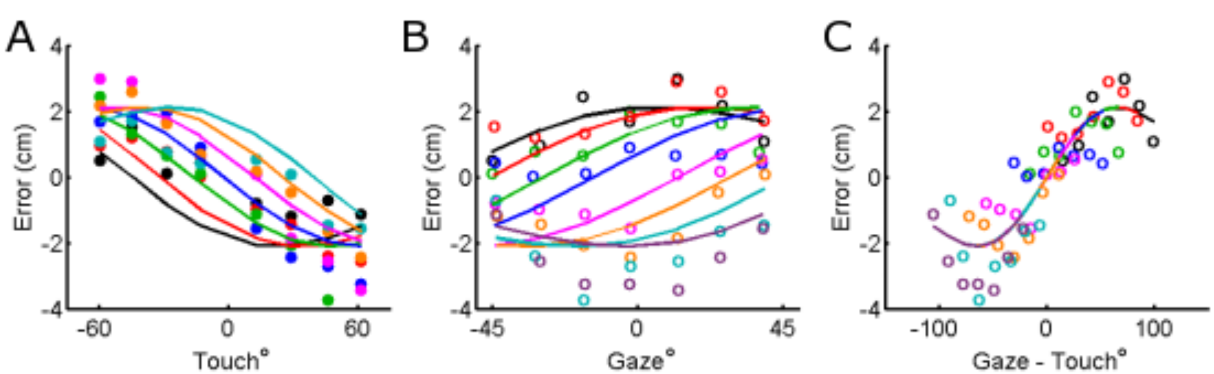

Figure 5.13. Gaussian-pull attractor model fit to the localization error data from the visual-line response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Inspection of the data in Figure 5.11 suggests that the effect of gaze-minus-touch may differ for different touch locations. Specifically, it appears that touches further from the navel were affected more than those closer to the navel. This was also suggested by the repeated measures ANOVA already reported, where a significant gaze-by-touch interaction indicated that touch locations further from the navel were more affected by gaze than those closer to the navel. The nonlinear attractor model was therefore modified to reflect this by adding an absolute value of touch term to the function so that the Gaussian pull was amplified linearly by the eccentricity of the touch relative to the navel:

$$E = (g - t) * b * N(g - t, 0, \sigma) * |t| \qquad \text{(Eq. 6, modified nonlinear-attractor mode)}$$

This modified nonlinear attractor model accounted for 86% of the variance in error data (see Figure 5.14). Although the absolute-value term was not specifically predicted, it is consistent with what we know about touch localization: touches closer to landmarks are localized more accurately. Thus it does make sense that touches closer to the navel would show less pull towards gaze.

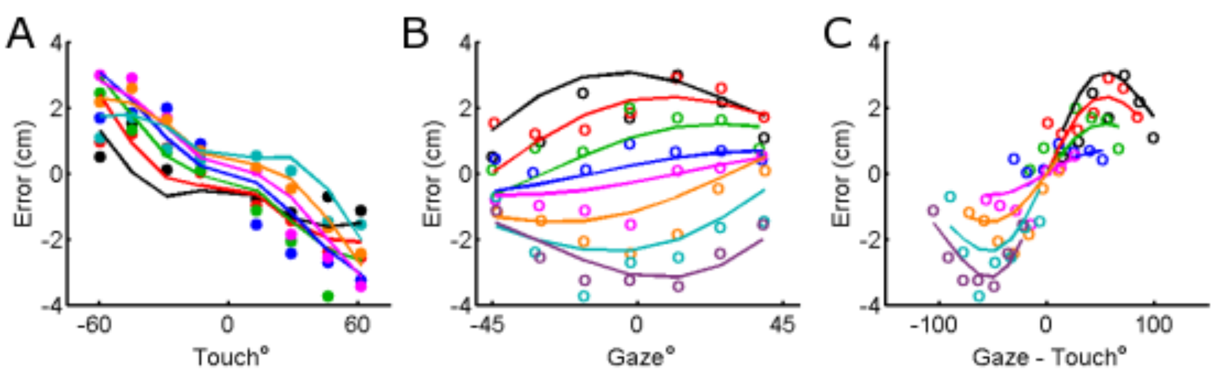

Figure 5.14. Gaussian-pull attractor with touches further from the navel attracted more (Eq. 6) model fit to data from the localization error data from the visual-line response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Model comparisons. The Akaike Information Criterion (AIC) was calculated for each model fitted to the data. The AIC measures the relative quality of statistical models allowing for comparisons between models with different numbers of parameters (Akaike, 1974). The raw value of the AIC itself is not informative, but the difference between AIC values for models explaining the same set of data is informative, better models have smaller AIC values. The AIC values are included in Table 5.1. Of all the models fitted, the modified nonlinear attractor model (eq. 6) has the smallest AIC value (118.82) and is thus the most likely of all the models to have caused the observed pattern of data. The relative likelihood of two models can be compared using the formula exp((AIC1 - AIC2)/2) (Burnham & Anderson, 2002). This is not equivalent to a hypothesis test, but if one model was at least 7 times more likely than another it would indicate considerably less support for the less likely model compared to the more likely model. If one model were 150 times more likely than another it would indicate essentially no support for the less likely model (Burnham & Anderson, 2002). Here, the most likely model, the modified nonlinear attractor model (eq. 6, AIC = 118.82) can be compared with the next most likely model, the shifter-plus model (eq. 3., AIC = 130.20). The modified nonlinear attractor model is exp((130.20 - 118.82)/2) = 295.6 times more likely than the shifter-plus model to underlie the data, indicating essentially no support for the shifter-plus model compared to the modified nonlinear attractor model.

Discussion of models for line-scale method. When participants reported the perceived location of touches on the torso using the visual-line response method there were localization errors related to both touch location and gaze, and there was an interaction between touch location and gaze on errors. To examine whether the shifter or attractor models (and the modifications of them described above) were more likely to have caused the pattern of errors observed a series of models were fit using MLE.

The shifter-plus model (eq. 3) predicts that localization error will be a linear function of gaze combined with an independent effect of touch location. This model accounted for 83% of the variance in localization error. In contrast, the attractor models (eq. 3-5) predict that localization error will be a function of the difference between the angle of gaze and of the angle of the touch on the body. The Gaussian-pull attractor model (eq. 4) accounted for 78% of the variance in localization error. However, an interaction between gaze and touch indicated that touch locations further from the navel were affected by gaze more than those closer to the navel. This finding was then incorporated into the attractor model in the modified nonlinear attractor model (eq. 5). After modification, the nonlinear attractor model (eq. 6) accounted for 86% of the variance in localization errors. Thus the modified nonlinear attractor model was the best fit to the data of all models tested. AIC values were calculated to directly compare models, and the modified nonlinear attractor model was by far the most likely to result in the pattern of data found.

Segmented-Space Method

Touch localization error data from the segmented-space method (SSM) are plotted in Figure 5.15 as a function of touch, gaze, and gaze-touch. A two-way repeated measures ANOVA was used to test for effects of touch and gaze. No significant effect of touch location was found (F (7,56) = 1.74, p = .22), and in contrast to the data obtained using the previous response methods, any effect is clearly not linear (see Figure 5.15A). A significant effect of gaze location was found (F(6, 48) = 6.10, p < .001), and trend analysis indicated that the effect of gaze on localization error was approximately linear (F(1,8) = 15.09, p = .005). There was a marginally significant interaction of gaze and touch (F(42, 336) = 1.70, p = .07). Simple effects one-way ANOVAs for each touch location with Bonferroni corrected p-value (.006) indicated that only touch locations 1 and 7 were significantly affected by gaze (p's < .003), and touch location 2 had a nearly significant effect of gaze (p = .007). The significant effect of gaze location is consistent with both the attractor and shifter models. These models were further analyzed using regression analysis.

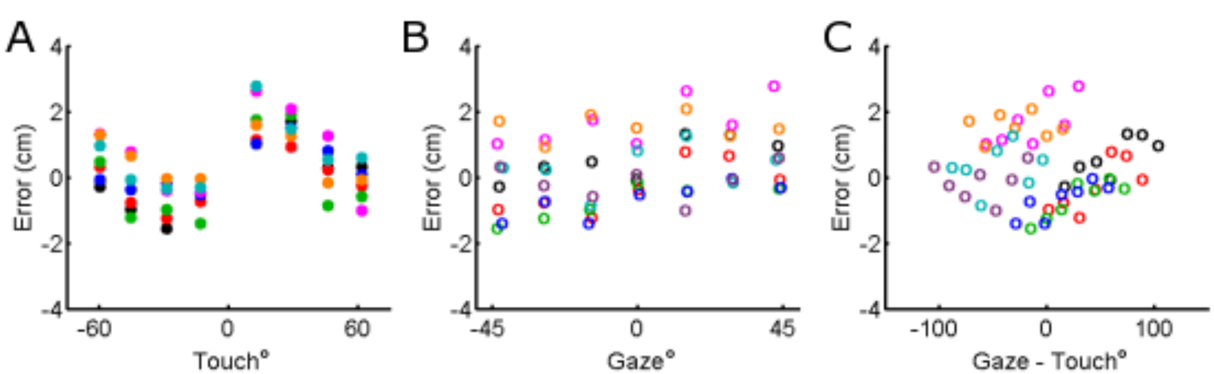

Figure 5.15. Localization error data from the segmented-space response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Table 5.2

MLE Regression Statistics for Segmented Space Data, Original Models

Model Name	Eq. Num.	Par 1	MLE (Std Err)	Par 2	MLE (Std Err)	RMSE	R^2	AIC
Shifter Models								
Shifter	1	*bg*	.011 (.005)			1.04	0.10	167.00
Shifter-Plus	3	*bg*	.011 (.005)	*bt*	.0059 (.003)	1.01	0.15	165.87
Attractor Models								
Attractor	2	*bgt*	-.0002 (.003)			1.09	0.00	172.27
Nonlinear Attractor	5	*bgt*	-.860 (.904)	*SD*	32.28 (17.78)	1.08	0.02	173.35
Modified Nonlinear Attractor	6	*bgt*	-.030 (.028)	*SD*	22.05 (0.10)	1.08	0.02	173.06

Shifter models. The shifter model predicts that error will be a function of gaze. Gaze did account for a small amount (10%) of variance in localization error. In addition, a linear effect of touch location did account for a small amount of variance (5%). The combined shifter-plus model (independent linear effects of gaze and touch) only accounted for 15% of variance in errors. This model's predictions are shown plotted through the data in Fig 16**.**

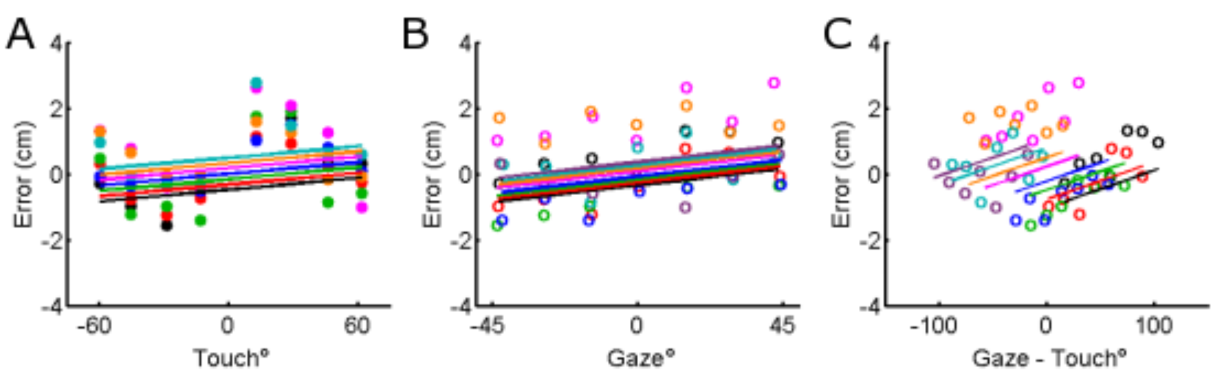

Figure 5.16. Shifter-plus model fit to the localization error data from the segmented-space response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Attractor models. The attractor model predicts that error will be a function of the difference between gaze and touch location. All versions of this model that were fit to the visual-scale data set accounted for very little (2% or less) of the variance in errors in this data set (see Figure 5.17).

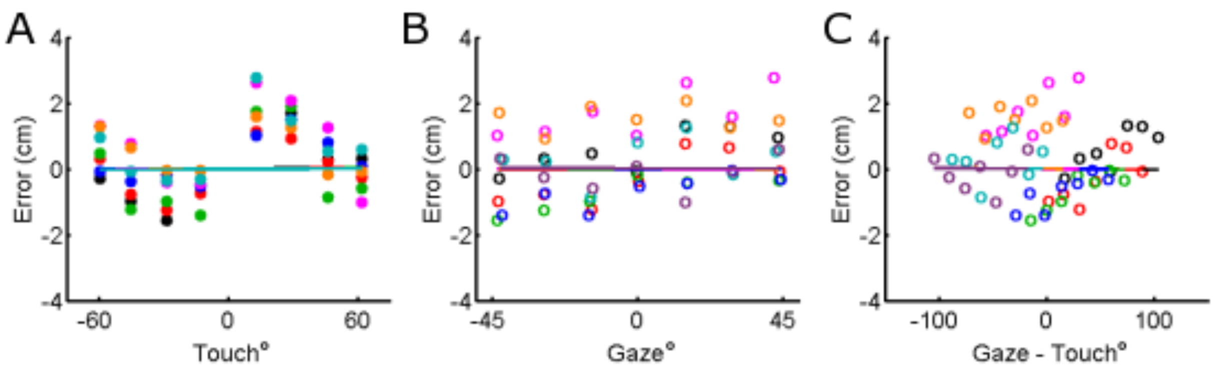

Figure 5.17. Linear Attractor model fit to the localization error data from the segmented-space response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.10.

Neither the shifter nor attractor models are a good fit to these data. The effect of touch location on localization error is clearly not linear (as the shifter-plus model predicts), nor is it equal and opposite of the effect of gaze (as the attractor model predicts). In every other data set examined here (pointing and line-scale methods) and from previous research (Pritchett et al., 2012), location of touch has had a linear effect on errors such that errors are toward the navel and are smallest for touches closest to the navel. In contrast, in this data set errors were largest for touches *closer* to the navel and were generally *away* from the navel. Previous research suggested that touches closer to body landmarks (like the navel) are localized more accurately and touches are perceived as closer to the landmarks than they actually are (Cholewiak et al., 2004; Cholewiak & Collins, 2003). In this data set, however, it could be that the end-points of the array rather than the navel were treated as reference landmarks. This is might be due to the response method used. Participants reported a number between 0 and 10 representing the area of skin vibrated. It could be that the numbers 0 and 10 and the locations associated with those numbers were used as reference points. That is, touches on the left part of the body were localized relative to the zero-location, and touches on the right were localized relative to the ten-location. Another possible explanation is that the number 5 represented the navel, and participants knew that they were never stimulated directly upon their navel (localization accuracy is very accurate at the location of body landmarks such as the navel), therefore, they never reported the number 5, and instead used numbers 0 to 4 for touches on the left and numbers 6 to 10 for touches on the right. This means that for the touches closest to the navel errors were only made away from the navel.

If the left or right half of the data in Figure 5.14A are examined independently, it appears that each is a linear function and that the left and right functions are offset vertically relative to one another. That is, if the left and right half of the data set were shifted vertically relative to one another, they would become a linear function. This pattern of compensatory vertical shifting can be modeled as a step-function. A step-function was defined:

$$step(t, a) = \{-a,\ if\ t < 0\,;\quad a,\ if\ t > 0 \qquad \text{(Eq. 7, step-function)}$$

This step-function was then added to the attractor and shifter models. On its own, the step function accounted for 29% of the variance in localization error.

Summary results of each of the models combined with the step-function are displayed in Table 5.3.

Table 5.3

MLE Regression Statistics for Segmented Space Data, Models including Step-Function

Model Name	Eq. Num.	Par 1	MLE (Std Err)	Par 2	MLE (Std Err)	Par 3	MLE (Std Err)	RMSE	R^2	AIC
Shifter Models										
Shifter w/ Step	1 + 7	*bg*	.011 (.004)			*a*	0.23 (.05)	0.93	0.32	153.58
Shifter-Plus w/ Step	3 + 7	*bg*	.011 (.003)	*bt*	-0.034 (.005)	*a*	1.83 (.19)	0.62	0.73	113.01
Attractor Models										
Attractor w/ Step	2 + 7	*bgt*	.018 (.003)			*a*	1.22 (.14)	0.71	0.62	126.36
Nonlinear Attractor w/ Step	5 + 7	*bgt*	7.09 (2.95)	*SD*	132.93 (76.11)	*a*	1.26 (.15)	0.71	0.62	127.8
Modified Nonlinear Attractor w/ Step	6 + 7	*bgt*	0.13 (.016)	*SD*	74.41 (10.96)	*a*	1.35 (.13)	0.61	0.74	112.13

Shifter models with step-function. The shifter model (eq. 1) postulates that error is a function of gaze. When combined with the step-function (eq. 7), this model predicted 32% of error in localization error. A linear effect of touch was then added to the model (so step-function (eq. 7), plus shifter-plus model (eq. 3) which then accounted for 73% of the variance in localization error. The step+shifter plus model predictions are plotted through the data in Figure 5.18.

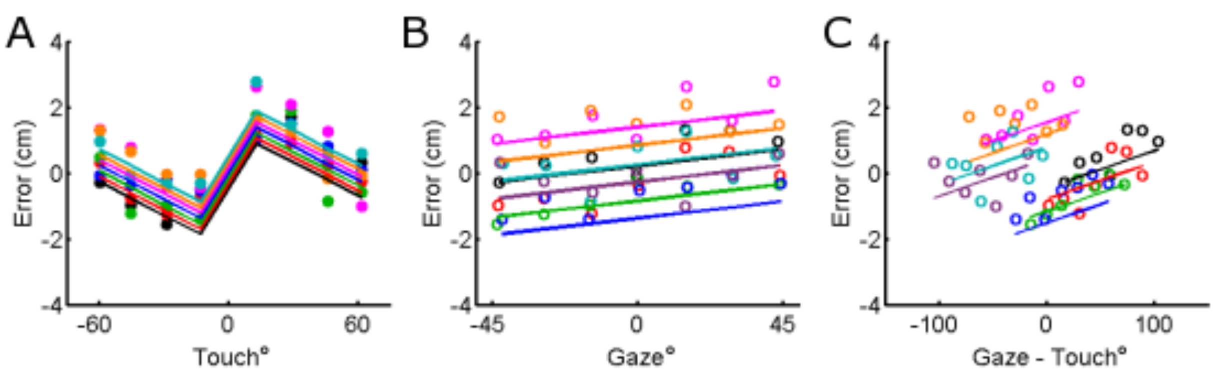

Figure 5.18. Shifter-plus model with step fit to the localization error data from the segmented-space response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.9.

Attractor models with step-function. The attractor model postulates that error is a function of the difference between gaze and touch. The step-function was added to all versions of this model that were also fit to the visual-scale data set. The linear attractor model (eq. 2) plus a step function (eq. 7) accounted for 62% of variance in errors (not shown). The same amount of variance was accounted for by the nonlinear attractor model (eq. 5) plus a step function (eq. 7) (see Figure 5.19). The step-function (eq. 7), plus the modified Gaussian-pull attractor model (eq. 6) (where touches further from the navel are attracted more) accounted for the most variance in localization, 74% (see Figure 5.20).

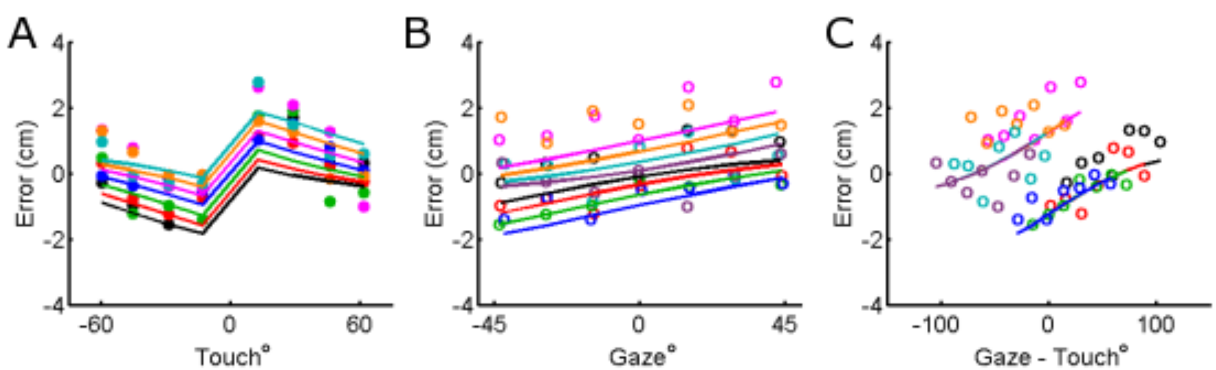

Figure 5.19. Gaussian-pull attractor model with step-function fit to the localization error data from the segmented-space response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.9.

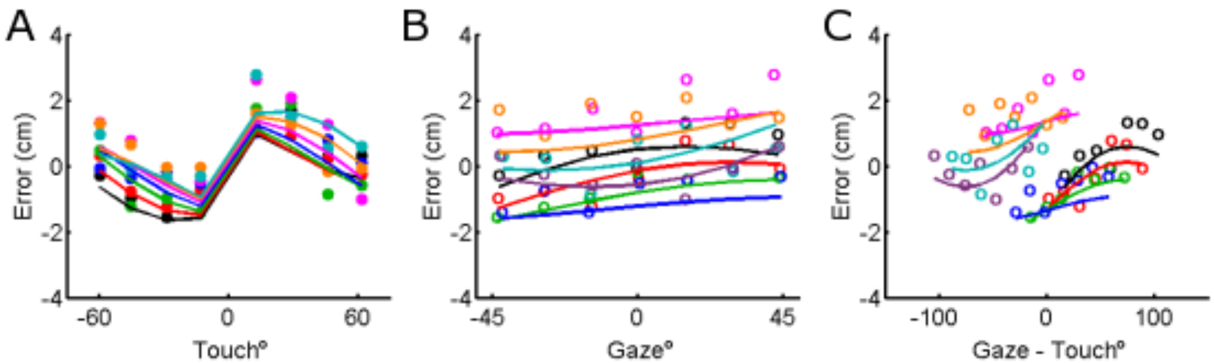

Figure 5.20. The modified Gaussian-pull attractor model with step-function fit to the localization error data from the segmented-space response method, plotted as a function of touch, gaze, and the difference between gaze and touch. Format as in Figure 5.9.

Model comparisons. The AIC was again used to compare the quality of each of the model's fit to the SSM data. AIC values are included in Table 5.2 and Table 5.3, for models without and with the step-function respectively. Without the step-function all models were a poor fit to the data (all $R^2 < .16$, all AIC values > 165). When the step function was included, all of the models fit the data better. The best model was the modified nonlinear attractor model (eq. 6) with step-function (eq. 7) ($R^2 = .74$, AIC = 112.13), followed by the shifter-plus model (eq. 3) with step-function (eq. 7) ($R^2 = .73$, AIC = 113.01). The modified nonlinear attractor model with step-function was only 1.55 times more likely than the shifter-plus model with step-function, so these two models are not really distinguishable, each are about equally likely to underlie the data. The next best quality model was the linear attractor model (eq. 2) with step-function (eq. 7) ($R^2 = .62$, AIC = 126.36), but the modified non-linear attractor model and shifter-plus model (both with step-function) were each much more likely (1230 times and 792 times, respectively). Therefore the AIC analysis indicates that either the shifter-plus model or the modified nonlinear attractor model (both with step-function) is most likely to explain the pattern of data observed.

Step-function vs. an attracted-to-ends model. The step-function may seem arbitrary. Indeed, it was certainly not predicted and was chosen mostly because it seemed to do a good job of accounting for the oddities in the data. Visual inspection of the data (Figure 5.14) suggested that if the data from the left and right half of the tactors were shifted relative to one-other the patterns would closely resemble the results in the line-scale method. When adjusted with such a step-function, the models fit to the line-scale data also provided a good fit to the SSM data. This offset does not affect the effect of gaze-location on localization error; notice that the gain-parameter (bg) fitted both with and without the offset is the same (bg = .011).

However, because the step-function seems arbitrary, and because we speculate that the offset may be caused by using the ends of the array as landmarks, we devised another function that could also account for the shift in localization errors away from the navel and toward the end points. This function is based on the nonlinear attractor function used to model localization error as being attracted towards gaze location, but instead of toward gaze this function pulls errors towards the end-points of the scale. The scale end-points of the scale are numbers 0 and 10; in degrees on the body (on average across participants in this study) the end-points are at approximately +/- 75 degrees. Therefore the attracted-to-end function was defined as:

$$(-75 - t) * \ b * N(-75 - t, 0, \sigma) + (75 - t) * b * N(75 - t, 0, \sigma)$$

(Eq. 8, to-ends function)

Where t = touch in degrees, bend is a gain factor for amount of pull towards the end, and σ is the width of the normally distributed attractor region.

On its own the to-ends function accounted for 56% of the variance in localization error. We added this model (Eq. 8) to each of the models we fitted to the line-scale data (Eq. 1 to 5). Summary results of MLE fits to these combined functions are displayed in Table 5.4. The models with this to-ends function did not account for the data as well as the models with the step-function. In addition, the AIC values for each of the models are nearly identical. The model explaining the data the best was the modified nonlinear attractor model (R^2 = .66, AIC = 123.99). However, it was only twice as likely as the shifter model (R^2 = .66, AIC = 125.36) to be underlying the data. The best model with the step-function included (the attracted-to-ends model with step-function), is 376 times more likely than the best model with the attracted to ends function.

Table 5.4

MLE Regression Statistics for Segmented Space Data, Models including Attracted to Ends Function

Model Name	Eq. Num.	Par 1	MLE (Std Err)	Par 2	MLE (Std Err)	Par 3	MLE (Std Err)	Par 4	MLE (Std Err)	RMSE	R^2	AIC
Shifter Models												
Shifter w/ to-ends	1 + 8	*bg*	0.011 (.003)			*bend*	31.47 (4.54)	*SDend*	66.29 (0.64)	0.69	0.66	125.36
Shifter-Plus w/ to-ends	3 + 8	*bg*	0.011 (.003)	*bt*	-0.025 (.007)	*bend*	13.30 (7.45)	*SDend*	50.97 (12.36)	0.69	0.66	126.78
Attractor Models												
Attractor w/ to-ends	2 + 8	*bgt*	0.011 (.003)			*bend*	24.49 (5.18)	*SDend*	62.40 (1.94)	0.69	0.66	125.19
Nonlinear Attractor w/ to-ends	5 + 8	*bgt*	3.85 (1.22)	*SD*	91.12 (35.82)	*bend*	25.33 (5.13)	*SDend*	62.26 (1.86)	0.68	0.67	125.63
Modified Nonlinear Attractor w/ to-ends	6 + 8	*bgt*	0.12 (.019)	*SD*	70.99 (11.84)	*bend*	10.17 (5.15)	*SDend*	49.52 (10.75)	0.67	0.68	123.99

Discussion of model fits to segmented-space response method. When participants reported perceived touch location using the SSM, gaze angle did have a significant effect on localization errors. However neither the shifter nor attractor models provided a good fit to the data (all $R^2 < .16$). It appears that there was something else affecting tactile localization that was not modeled by either equation. It could be that the SSM response method led to the endpoints of the scale being used as reference points, leading to more accurate localization for touches near the ends of the scale and touches near the middle being shifted towards the end rather than towards the navel.

This effect was modeled using a step-function and an attracted towards ends function. When the step-function was added to the shifter and attractor models, fits improved substantially, explaining up to 74% of the variance in localization error. However, even when including the step-function, the modified nonlinear attractor model (eq. 6) and the shifter-plus model (eq. 3) were about equally likely to explain the data. When combined with the set of shifter and attractor models the attracted-to-ends function (eq. 8) did not do as well at explaining the data as when the step-function (eq. 7) was included. And again, the attractor models and shifter models were about equally likely. Therefore, for the SSM data, we cannot conclusively determine whether touch localization is better described as shifting in the direction of gaze or as being attracted towards gaze. Both are about equally likely based on this data set.

Discussion

Tactile localization errors from three response methods were examined in the same subjects to determine whether gaze causes a shift in perceived touch location in the same direction as gaze (the shifter models) or if touches are attracted to the location of gaze (the attractor models). Though on paper these models make different predictions, in practice it became difficult to distinguish between these two classes of models. This is because gaze is not the only factor affecting accuracy of touch localization. The analysis reported here highlights the importance of many other factors, including the method of response and the location of touches.

Method of response had a large effect on the accuracy of tactile localization. When pointing to the location of touch, responses were much more accurate than other methods of response. In addition, there were no effects of gaze or touch location for the pointing response method. This suggests that gaze is not a primary reference point when the response is made by pointing, at least for touches to the body torso. Previous research has shown effects of gaze on pointing to touches to the arm (Harrar & Harris, 2010) and fingers (Mueller & Fiehler, 2014a). In these studies, the parts of skin touched were within the visual field, perhaps encouraging gaze-related coding. In previous studies with touch locations outside of the visual field we have found an effect of gaze (chapters 2 through 4), but those have used the visual-line response method, which could also encourage gaze-related coding.

For the visual-line and segmented-space methods, gaze did have a significant effect on localization error. Furthermore, the size of the effect noted using these two methods were similar. However, even these two methods did show different effects of touch location on error. In the visual-line response method, touches closer to the navel were localized more accurately, and all touches were perceived as shifted toward the navel. The SSM showed a near opposite pattern, in which touches close to the navel were localized the least accurately, and perceived touch locations were shifted away from the navel. These differing patterns may reflect differences in reference points used by participants when doing a visually-referenced versus a body-referenced task. Previous research has shown that touch localization is usually more accurate near body landmarks that are used as reference points, and that touches further from landmarks are perceived as closer to those landmarks than they actually are (Cholewiak et al., 2004; Cholewiak & Collins, 2003). For touches on the front of the torso we assumed that the navel would be the most important landmark. The visual-line data (and to some extent the pointing data) support this assumption: touch localization was most accurate and reliable for touches near the navel and other touches were reported as shifted towards the navel. In addition to the anatomical reference point, the visual-scale itself may encourage the middle of the scale to be used as a reference point: the slider used to indicate location always started at the middle of the scale, making the middle location unambiguous. In contrast, for the SSM data the end-points appeared to be the important reference point: touches at the end of the scale were localized more accurately, and the others were reported as shifted towards the ends of the scale. Because the only difference in this task, compared to the others, was the method of response (participants reported a number between 0 and 10 to indicate the location), we speculate that the numbers 0 and 10 were used as reference points. This highlights the importance of response method on the reference points used in touch localization.

The initial purpose of this set of experiments was to examine whether perceived touch locations are shifted in the direction of gaze (the shifter model, consistent with using an underestimated gaze signal as a reference point), or whether touches are perceived as closer to gaze than they actually are (the attractor model). The shifter model predicts errors will be a function of gaze and the attractor model predicts errors will be a function of the difference between gaze and touch. For the visual-line response method a linear effect of gaze (the shifter model, Eq. 1) only accounted for 2% of variance in localization errors. In contrast, a linear function of the difference between gaze and touch (the linear attractor model, eq. 2) accounted for 68% of variance in localization errors. However, this effect may be primarily driven by a linear effect of touch location, which is why an independent linear effect of touch was added in the shifter-plus model. The shifter-plus model (eq. 3) then accounted for 83% of variance in localization error. With respect to the attractor model, the effect of the difference of gaze and touch did not appear to be linear. A model which predicts that gaze attracts perceived locations with a strength that declines with the distance between the location and gaze (the nonlinear-attractor model, Eq. 5) provided a good fit to the data from the visual-scale method, explaining 78% of variance in localization errors, but an even better fit was found by adding that touches further from the navel are affected more (the modified nonlinear attractor model, Eq. 6), which explained 86% of variance in localization error. This final model provided the best fit of any we tested for the visual-line data.

Analysis of AIC values for each model indicated that the modified nonlinear attractor model was the most likely to explain the data, and was nearly 300 times more likely than the next-most likely model (the shifter-plus model). This allows for a decisive conclusion that, at least when touch localization is reported with the visual-line method, perceived touch locations are shifted towards the location of gaze rather than in the direction of gaze, as we have previously speculated.

For the SSM data, no model provided a good fit until a step-function was added to the models. This multi-factor function then accounted for the fact that touches on the left were shifted to the left and touches to the right were shifted to the right. Once this function was added to the models, both the shifter-plus (eq. 3 plus eq. 7) and the modified nonlinear attractor model (eq. 6 plus eq. 7) accounted for a large portion of variance in errors (66 and 68% of variance, respectively). AIC analysis found that the modified nonlinear attractor model with step-function (eq. 3 plus eq. 7) was only 1.5 times more likely to explain the data than the shifter-plus model with step-function (eq. 3 plus eq. 7). Based on this, there is not enough evidence to conclusively determine whether touch locations were shifted towards gaze or in the direction of gaze. However, the attractor model is slightly more likely than the shifter model, and since the attractor model was conclusively supported using the visual-line method I speculate that it is probably also the true effect operating in the SSM. The attractor model is also more parsimonious with previous research[4] where we found that touches on the back of the body were perceived as closer to the location of gaze (with head rotated clockwise, touches on the right part of the body were reported as further counter-clockwise than they were with the head centered on the body). This finding suggested that touches might be attracted towards gaze rather than shifted in the direction of gaze. However, we could not rule-out the possibility that touches to the back of the body are coded differently than those on the front. For example, touches on the back may be referred to the

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[4] The experiments conducted on the back (Chapter 5), as well as previous experiments conducted on the front of the torso (Chapter 3, Pritchett et al., 2012), used the visual-line scale similar to the one used here. However, in those analyses we choose not to analyze error, and instead analyzed the difference in localization when touches were applied with the head turned from the location reported with the head centered on the body. This is because we were not convinced that the response method used could really test for "accuracy" (there are errors related to response in addition to errors related to perception). However, for purposes of testing the shifter model versus the attractor model, both models make the exact same predictions for this "difference from gaze-centered" measure. The two models only made differing predictions for the absolute error. This is one reason we used more response methods, including pointing and the SSM. In addition, we modified the instructions to participants slightly for the visual-scale method. Previously, participants were asked to anchor the touches at the end of the array to the end-points of the visual scale. This results in errors for the touches on the ends of the scale to only have errors possible in one direction: toward the middle. In the current study, participants were asked to anchor the end points of the visual-scale to body locations that were 4 cm beyond the final touch locations (the reflective markers numbered ii and iii in Figure 5.1), thus errors were possible in either direction for all tactor locations.

front before coding. This possibility was reinforced by findings that the skin on corresponding points of the front and back of the body are linked (tactile vibration sensitivity for locations on the front are impaired when a corresponding point of the back is vibrated) (D'Amour & Harris, 2014). However, when considered alongside the current findings, it seems more likely that touch locations are indeed attracted towards gaze location rather than shifted in the direction of gaze.

In previous research (chapter 3, Pritchett et al., 2012) we found that the direction of the effect of gaze depends on whether the task is dynamic (causing towards/in direction of gaze effects) or static (causing away from gaze effects). We reasoned that this most likely indicates that the reference frame used in coding touch location depends on the task: when the task is dynamic the location of gaze is used as a reference point, and when the task is static the body straight-ahead is used as a reference point. We reasoned that a single underestimated representation of the gaze angle could cause both the location of gaze and the location of the body straight-ahead to be misrepresented, causing any locations coded relative to those points to also show those effects. Though the attractor model suggests that these results are not due to the underestimated gaze signal but instead an attraction towards the gaze direction, it still suggests that different reference frames are used depending on whether the task involves remembering a location during a move, as in our dynamic paradigm, or just an immediate reporting, as in our static paradigm. In addition, our experiments reveal further influences that depend not only on static versus dynamic conditions, but also on the response method. Response methods that require a visually based judgment are associated with different errors from those that require body-based judgments and those that require action have a different pattern of errors again. The attractor model would suggest that locations are coded as closer to the reference point used than they actually are (i.e. gaze in this case) when locations are perceptually reported. This suggests a general underestimate of touch location relative to the reference points used, reminiscent of foveal bias in vision (Kerzel, 2002; Mateeff & Gourevich, 1983; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999). This is also consistent with our speculation regarding the SSM data: touches are coded as closer to the reference points “0” or “10” and at the same time coded as closer to the location of the gaze reference point. For the pointing response, no effect of gaze direction was found, suggesting that representing touch locations for action does not require gaze-related coding.

Conclusion

The experiments described here tested whether gaze effects touch locations in a dynamic task by shifting them all in the direction of gaze (as an underestimated representation of gaze would cause), or by attracting locations towards the location of gaze. Results suggest that touch locations are attracted towards the location of gaze, suggesting a general attraction of locations towards reference points especially for perceptual measures.

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Chapter 6. General Discussion

The research described in this thesis demonstrates several new findings regarding the effects of gaze position on the perceived location of touch on the body. First, in chapter 2, I showed that, when manipulated in the same way, both eye and head angle have the same effect on touch localization. This finding indicates that the effect is likely a result of *gaze angle* rather than independent effects of eye and head orientation. This is consistent with results in the visual (Yamaguchi & Kaneko, 2007) and auditory (Lewald & Ehrenstein, 1998) literature which also finds that eye and head angle have the same effect on spatial localization.

In chapter 3, I demonstrated that differences in the experimental procedure can lead to opposite directions of the effect of gaze on touch localization: when no movement was made in between touch and response, gaze angle shifted the perceived location of touches in the opposite direction to gaze, whereas when a head movement was made between touch and response, the effect was in the same direction as gaze. However, this result does not appear to be a result of spatial updating. In experiment 3, (which is most similar to the experiment by Henriques, Klier, Smith, Lowy, & Crawford (1998) which demonstrated gaze-centered updating of visual locations) when gaze orientation was centered for touch presentation and then gaze was turned before the response there was no shift in the perceived location of touch. Thus it is the orientation of gaze at the time of the touch presentation that matters, and subsequent movements of gaze do not impact localization. It is likely that the opposite directions of the effects indicate that the touch location was coded in different reference frames depending on the task: when no movement was made between touch and response touches appeared to be localized in a body-centered reference frame, whereas when a movement was made between touch and response touches were localized in a gaze-centered reference frame. A model based on the idea of an underestimated gaze angle was proposed that could explain errors in either direction. As shown by Hill (1972) and Morgan (1978) an underestimated representation of gaze angle can cause a misperceived location of the body straight ahead. Either that misperceived body straight ahead or a misperceived location of gaze angle could then be used a reference point for spatial localization. Coding relative to one or other of these two erroneous reference points would then cause opposite directions of effects, as we found.

Next, in chapter 4, I showed that touches on the back of the body were also affected by gaze angle in the dynamic condition where a head movement was made between touch and response. In the static condition, where no head movement was made, there was also an effect of head orientation, but it was much smaller than observed for the dynamic condition or for the front of the body. Since the static condition was thought be associated with body-centered coding in chapter 3, I argued that the reference point for the back of the body was not shifted by gaze, leading to no effect of gaze on the back in that condition. In the dynamic condition the effect that was found was not in the direction that I expected. This indicated that either the model of how gaze angle effects touch location was incorrect (i.e., the shift was not due an underestimated gaze angle) or that touches on the back were localized in a different manner than those on the front (i.e., locations on the back were referred to the front before being coded relative to gaze).

Finally, in chapter 5, I directly examine whether the effect of gaze angle on touch localization was due to an underestimated representation of gaze angle, or if it was due to misperceiving the location of a touch relative to the gaze reference point analogous to the Retinal Magnification Effect (RME), which has been used to explain the effect of gaze angle on visual localization (Bock, 1993; Henriques et al., 1998) . If the effect were due to an underestimated representation of gaze then the amount of error should be proportional to the angle of gaze on the body, whereas if the effect were due to misperceiving the distance between the touch and gaze, the effect should be a function of the distance between gaze and touch angle. The error in touch localization was found to be better described as a function of the distance between gaze and touch angle (particularly when a visual scale was used for response), indicating that touch locations are shifted toward the location of gaze, rather than gaze angle being misperceived on the body. Other response methods showed either no effect of gaze angle (when pointing) or errors were not well described by either model. This indicates that the method of response has a large impact on the reference frames used in tactile spatial localization. This could indicate that locations coded for perception, but not those coded to guide actions are coded in gaze-related reference frame.

Comparison to Other Research

In the time between when the first three experimental chapters (chapter 2, 3 and 4) in this thesis were conducted and published (Pritchett, Carnevale, & Harris, 2012; Pritchett & Harris, 2011) and the last experiment chapter was conceived, other researchers published important findings regarding the effect of gaze angle on touch localization. For example, Mueller & Fiehler (2014b) examined how a gaze shift between touch presentation and response affected tactile localization relative to visual localization. Touches were applied to the arm and visual comparison stimuli were projected onto a surface occluding the arm from view. Participants reported whether the tactile stimulus was perceived to the left or right of the visual comparison. Whenever gaze was held constant after the presentation of a touch, tactile and visual locations were affected by gaze *differently*, whereas when a gaze shift was made after presentation of a touch, gaze direction affected the visual and tactile location *similarly.* These findings indicate that when gaze is held constant after presentation of a touch, tactile and visual location are processed differently by the brain, i.e., in different spatial reference frames. However, when a gaze shift is made between a touch and the subsequent response, tactile and visual locations appear to be coded in the same spatial reference frame, presumably in a gaze-centered reference frame. In a second report (Mueller & Fiehler, 2014a) they found that when the response was made by reaching (rather than by a tactile-visual comparison) a gaze movement between the touch and the response led to gaze-related errors, while when no gaze movement was made between touch and response no gaze-related errors were found. In addition, Mueller and Fiehler

(2014a) found that if the part of the body receiving the touches was moved after touch presentation, gaze-related coding was triggered.

Their conclusion that effector (eye, head or body) movement triggers gaze-centered coding is consistent with my conclusion from Chapter 3 (Pritchett et al., 2012) where moving the head between touch and response reversed the direction of the effect, indicating a switch in the reference frame used. However, Mueller and Fiehler (2014a, 2014b) also found that, after an effector movement, gaze direction caused a shift in perceived touch location in the direction *opposite* to gaze (that is, in the same direction as gaze was found to affect visual localization by Henriques et al. (1998), while I found that touch localization was shifted in the *same* direction as gaze if a gaze movement was made between touch and response. That is, Mueller and Fiehler's results are consistent with the RME (shifts away from fovea) described in the visual literature (Bock, 1993; Henriques et al., 1998), while my results and those of Harrar and colleagues (Harrar & Harris, 2009, 2010; Harrar, Pritchett, & Harris, 2013; Harrar, 2010) were in the opposite direction to the RME (towards the fovea). It is difficult to determine why we find opposite directions of effects under these circumstances. It is unlikely that the difference is a result of type of tactile stimulation used since Mueller and Fiehler (2014a, 2014b) used solenoid touches, which was the method used by Harrar and Harris (2009, 2010), Harrar et al. (2013), Harrar (2010), and in Chapter 2 of the present work (Pritchett & Harris, 2011). It is also unlikely that the response method caused the difference as Mueller and Fiehler used both a reaching task (2014a) and a perceptual comparison task (2014b), and Harrar also used both of these tasks. Harrar's and my results may be more related to the foveal bias effect where very briefly presented visual stimuli are perceived as closer to the fovea than they actually are (Kerzel, 2002) rather than the RME, and could thus be a result of using very briefly presented tactile targets. However, Mueller and Fiehler also used very brief tactile targets. The most likely cause of the different directions of effects is that in Harrar and my studies eye position was not tightly controlled after presentation of touch. Participants in these studies were allowed to move their eyes freely to aid in making accurate responses. In contrast, Mueller and Fiehler did not allow participants to move their eyes freely during the response phase. This suggests that gaze shifts made during the response phase may further alter the spatial reference frames used in representing tactile localization. This possibility should be investigated in future research.

Response Method Impacts Coding Reference Frame

In chapter 5, I found that the method of response had a large impact on gaze-related spatial localization errors. This is in contrast to Harrar (2010) who reported that gaze direction affected spatial localization in the same manner regardless of the response method used. She found that independent of whether visual comparison (Harrar & Harris, 2009) or pointing (Harrar & Harris, 2010) was used, perceived touch location was shifted in the direction of gaze. In contrast, I found no consistent effect of gaze when pointing to touch locations on the torso direction. This could be because touch locations were outside of the visual field. Perhaps if touch locations were within the visual field, as they were in Harrar and Harris (2010), we would have found a significant effect of gaze direction. This is also consistent with the results we found in chapter 3 where only touch locations on the same side as gaze direction were affected by gaze. Another possible explanation is that the part of the body touched caused the differences. Possibly, touches to the arms are coded in a gaze-dependent reference frame even when an action response is made, but touches to the torso remain in a somatotopic reference frame unless a perceptual response (as opposed to a motor response) is made.

Effect is Not a Result of Underestimated Gaze Angle

In Chapter 3, I presented a model explaining the effect of gaze direction on touch localization as resulting from an underestimated gaze signal. However, in Chapter 5 I found that the effect is more likely to be a result of misperceiving the spatial location of touches relative to gaze rather than an effect of underestimating gaze angle per se. Errors were better described as a function of the distance between gaze and touch than as a function of gaze angle. This indicates that touch locations are shifted towards gaze rather than shifted in the direction of gaze. As a result of the findings in chapter 5 I suggest an update to the model presented in chapter 3. Rather than touch locations being shifted in the direction of gaze for gaze-centered coding and in the opposite direction for body-centered coding, I propose that touches are shifted toward the reference point used. Thus, in the dynamic condition of chapter 3, touches were coded relative to gaze and shifted towards gaze and in the static condition of Chapter 3, touches were coded relative to the body straight-ahead and shifted towards the body straight-ahead. Therefore, the conclusion in Chapter 3 that moving gaze in between touch and response triggered a change in reference frame used in coding the location remains the most likely explanation for those data.

Limitations

In all of the experiments described here, only one or two dimensions of space are considered. The third dimension (vertical) was not considered and should be examined in future research and analysis. Indeed, if touch locations are coded relative to gaze then the touch locations on the torso in Chapters 3 – 5 would have a large vertical component (as touches are considerably lower than gaze angle) in addition to the horizontal component(s) considered in the analyses presented here. This point may be even more relevant for touch locations on the back.

Throughout this work we present the effects and errors in touch localization as effects in the *perception* of touch location. It is important to point out that these errors may be due to the *response* only, and that the actual perception of touch location may not be affected. However, there are some reasons to believe that at least some of the errors relate to *perception.* For one, errors are found in nearly every response method used, accept for pointing in Chapter 5, though other researchers have shown effects related to pointing (Harrar & Harris, 2010; Mueller & Fiehler, 2014a). In addition, in Chapter 3 if effects were only due to how the response measure was used, we would have expected to see significant effects in Experiment 3 when touch was *reported* with gaze eccentric but *perceived* with gaze centered. That touch localization was not affected when response was made with gaze eccentric suggests that errors are in fact due to *perception.*

Overall Conclusions

The work described in this thesis demonstrates that behavioral work can elucidate the coding mechanisms used in the brain. Although neurophysiological and neuroimaging work has shown that stimuli locations are coded in multiple reference frames in the brain, behavioral work such as this is required to show that those representations are actually perceptually and behaviorally relevant.

This work also has practical implications. Tactile displays similar to the array of vibrators on the tactor array used in chapters 3 through 5 are used to provide spatial orientation cues for aviation pilots and in other spatial navigation situations (Gemperle, Ota, & Siewiorek, 2001; Jones, Lockyer, & Piateski, 2006; Tsukada & Yasumura, 2004; van Erp, 2001). In these applications it is assumed that a given tactor at a fixed location will always be perceived in the same location, and can thus provide spatial navigation information to the wearer. However, in these applications it may be very important to know that the perceived location actually depends on the orientation of gaze. Operators should heed these results and urge wearers to orient gaze in a fixed location before interpreting the information provided by the tactile display, especially when knowing the precise location may make the difference between life and death as in aviation and military applications.

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Appendix A: Disclaimer for Coauthored Chapters

Chapters 2 and 3 in this dissertation have been published (see Appendix C and D), both with coauthors. My supervisor Laurence Harris is coauthor on both. He has played a large roll in the inception, design, interpretation, and writing of this entire dissertation. Michael Carnevale is coauthor of the publication of Chapter 3. Michael assisted with seting up of the experimental apparatus, collecting data by running subjects, and provided some input on the written chapter. Nonetheless, I have done the majority of the work in this dissertation. I conceived of most of the experiments and I set up the apparatus used in chapters 3, 4 and 5, including the gaze and body tracker used in Chapter 5. I programmed all of the experiments and ran most of the participants. I completed all of the data analysis for every chapter, and I wrote the first draft of all of the chapters in this dissertation.

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Appendix C: Pritchett & Harris 2011

Pritchett, L. M., & Harris, L. R. (2011). Perceived touch location is coded using a gaze signal. *Experimental Brain Research*, *213*, 229–234. doi:10.1007/s00221-011-2713-0

Exp Brain Res (2011) 213:229–234
DOI 10.1007/s00221-011-2713-0

RESEARCH ARTICLE

Perceived touch location is coded using a gaze signal

Lisa M. Pritchett · Laurence R. Harris

Received: 12 October 2010 / Accepted: 26 April 2011 / Published online: 11 May 2011

Abstract The location of a touch to the skin, first coded in body coordinates, may be transformed into retinotopic coordinates to facilitate visual-tactile integration. In order for the touch location to be transformed into a retinotopic reference frame, the location of the eyes and head must be taken into account. Previous studies have found eye position–related errors (Harrar and Harris in Exp Brain Res 203:615–620, 2009) and head position–related errors (Ho and Spence Brain Res 1144:136–141, 2007) in tactile localization, indicating that imperfect versions of eye and head signals may be used in the body-to-visual coordinate transformation. Here, we investigated the combined effects of head and eye position on the perceived location of a mechanical touch to the arm. Subjects reported the perceived position of a touch that was presented while their head was positioned to the left, right, or center of the body and their eyes were positioned to the left, right, or center in their orbits. The perceived location of a touch shifted in the direction of both head and the eyes by approximately the same amount. We interpret these shifts as being consistent with touch location being coded in a visual reference frame with a gaze signal used to compute the transformation.

Keywords Tactile coding · Eye position · Head position · Gaze · Visual representation of body · Coordinate transformations

L. M. Pritchett (✉) · L. R. Harris
Department of Psychology & Centre for Vision Research, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada
e-mail: lmpritch@yorku.ca

Introduction

A challenge in understanding multisensory integration is how the human brain integrates spatial information from different modalities all coded in different reference frames. One theory is that there is a multimodal map that integrates multisensory information into a single spatial representation. To transform between body coordinates and retinotopic coordinates, the brain must consider the current posture of the body as well as either (1) the location of the eyes and the head or (2) the location of gaze (because gaze is the sum of eye and head positions). If tactile information were coded in retinotopic coordinates, then any errors in the representation of the position of either the eye or head would cause systematic shifts in touch localization.

Errors in coding the position of the eyes (Harris and Smith 2008) and systematic shifts in tactile localization related to eye and head positions have previously been demonstrated (Harrar and Harris 2009, 2010; Ho and Spence 2007), suggesting that touch is indeed coded in retinotopic coordinates. Eye position was found to cause shifts in the location of touch in the same direction as eye position (Harrar and Harris 2009), while head position has been found to cause shifts in the *opposite* direction (Ho and Spence 2007). This would suggest that eye and head positions are coded separately in the sensory transformation, with the signal for eye eccentricity being underestimated and the signal for head eccentricity being overestimated. Large differences between the techniques using head and eye positions in these studies make comparing their results difficult. The research on eye position used solenoid touches on the arm while the head position research used vibration on the torso. The two studies also had substantial procedural differences. The present study allows for comparison of the effects of head and eye eccentricity on touch localization directly.

Errors due to eye and head positions have been found for auditory (Collins et al. 2010; Goossens and van Opstal 1999; Graziano 2001; Kopinska and Harris 2003; Lewald 1998; Lewald and Ehrenstein 1996a, b, 1998), visual (Harris and Smith 2008; Kopinska and Harris 2003; Wexler 2003), and proprioceptive (Fiehler et al. 2010; Lewald and Ehrenstein 2000) localization, suggesting that spatial information across all these senses may be integrated into a single common retinotopic reference frame.

The majority of this research has investigated either the effect of eye position or the effect of head position on spatial localization but, to our knowledge, only one study has directly compared the effects of eye and head positions and how they combine. Lewald and Ehernstein (1998) reported that both head and eye position affected the perceived location of a sound and that both effects were in the same direction (opposite to the direction of the head and eye) and of approximately the same magnitude. When the eyes and head were in opposite directions (e.g., eyes 30 degrees left and head 30 degrees right, such that gaze remained straight ahead), the effects appeared to cancel out indicating linearly combining effects.

We investigated the effects of eye and head position on the perceived location of touch. Participants held their head to the left, right, or center of their body and their eyes to the left, right, or center in their head while a touch was applied to the arm. Participants reported the position of the touch relative to a visual probe. They centered their eyes and heads before the probe was presented in order to avoid any possible effects of eye and head positions on the perceived location of the probe.

Methods

Participants

Four women and six men with an average age of 32 years participated. One male participant was left handed, and all others were right handed. All had normal or corrected-to-normal vision. Experiments were approved by the York Ethics board.

Apparatus

The touch apparatus consisted of two solenoids encased in a box with pins facing upwards. When power (amplified 5 volt signals from a CED1401 interface box (Cambridge Electronic Design, Cambridge, UK) controlled by a PC) was delivered to each solenoid its pin extended about 2 mm from the surface of the box for 50 ms. The pins were located at approximately 6 and 11.5 cm from the subject's wrist (or 2.5 degrees left and 3.5 degrees right of straight ahead) (see Fig. 1).

A flat screen computer monitor (54 cm, resolution 1600 × 1200 pixels) was positioned vertically 5.2 cm behind the solenoids and 29 cm from the viewer. It was used to display gaze and head fixation points as well as a probe line used for comparison with the perceived location of the touch. The probe line was a 15 cm long, one pixel wide, red, vertical line positioned on the screen with its top 5.5 cm (10.7 degrees) below the gaze fixation points. The bottom of the probe line was at the bottom of the screen, which was at the same height as the arm when positioned over the solenoids.

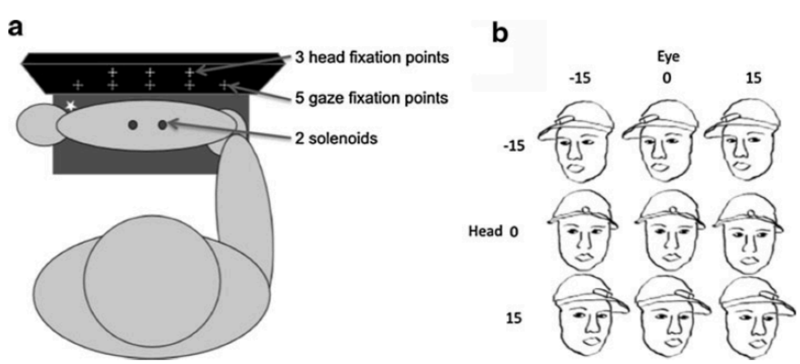

Fig. 1 Apparatus set up and experimental conditions. **a** Touch locations were at 6 degrees left and 7 degrees right from straight ahead, or 6 and 11.5 cm from a star on the box that encased the solenoids. The star was approximately aligned with the wrist crease. The screen displaying fixation points and a probe line was positioned directly behind the touch box, 5.2 cm behind the solenoids and 29 cm from the viewer. The bottom edge of the screen was level with the top of the solenoids. **b** For each of three head positions (15 degrees to the left, 15 degrees to the right, and centered), three eye positions were used, such that the eyes could be centered or at 15 degrees to the left or right in their orbits. Nine combinations of eye and head positions led to five different gaze positions, 30 degrees to the left and right, 15 degrees to the left and right, and centered. A laser mounted to the head allowed for precise control of head position

Controlling head and eye position

Participants wore a baseball hat with a laser pointer attached to the rim. They aligned the laser beam with head fixation targets presented on the screen. Three head fixation points were used: −15° (left), 0° (straight ahead) and +15° (right). For each head fixation, three eye fixations were used: −15° (left in head), 0° (centered in head) and +15° (right in head). Thus, five gaze fixation points were needed (−30, −15, 0, +15, +30°, relative to the body straight ahead). Head fixation points were positioned at the approximate height of the laser point projected from the hat and gaze fixations were positioned 3 cm below the head fixations at eye height. Figure 1 shows the arrangement of the apparatus and the head and gaze fixation points.

Procedure

Participants were seated in front of the apparatus and wore headphones to muffle the sound of the touches and a baseball hat with mounted laser pointer. The hat was adjusted such that the laser pointed directly at the "centered" head fixation point when their head was oriented straight ahead. Participants then positioned their arm across the touch box and aligned their wrist crease with a star on the box (see Fig. 1).[1]

Each trial began with head and eyes centered. A head fixation cross was displayed in one of the 5 locations, and the participant was allowed 1 s to turn their head and point the head-mounted laser at the cross. Next, a gaze fixation point was displayed which the participant foveated. One second later, both the gaze and the head fixation points were removed from the screen. The subject maintained their head and eye position while a touch was administered at one of the two locations on the arm. A central fixation point was presented 500 ms after the touch for duration of 2 s, directing participants to recenter their head and eyes before responding. After the head and eyes were recentered, a vertical line probe was presented. Subjects were allowed to move their eyes to the line to make a judgment regarding whether the line was to the left or right of where they were touched. The line remained visible until a response was made, using left and right foot presses. The subject's response initiated the next trial.

The position of the line probe was controlled by a best PEST adaptive procedure (Pentland 1980). For the first trial of each condition, the location of the reference line on the screen was chosen randomly. In subsequent trials, the reference line was moved to the left or right depending on the participant's response to the previous occurrence of that condition. Step size was initially 100 mm and was halved after each reversal and doubled after three consecutive steps in the same direction. The minimum step size was 1 mm. Once the minimum step size was reached, the PEST staircase terminated for that condition and the final location of the probe line was taken as the perceived touch location. Staircases for each of the 18 conditions were interleaved and randomly selected during testing. The entire session lasted approximately 50 min.

[1] Exact lining up of the arm on the stimulation box was not necessary as judgments were made between the location of the solenoids and the reference line on the screen which were fixed relative to each other.

Results

Figure 2 plots the effect of gaze on perceived touch location. A three-way repeated measures ANOVA was conducted for effects of touch location, eye eccentricity, and head eccentricity. Eye position significantly affected perceived touch location (F (2,18) = 4.37, P = .033, η_P^2 =.33). When the eyes were to the left in their orbits, the perceived location of the touch appeared displaced to the left, and when eyes were to the right in their orbits, the perceived location of the touch was displaced to the right relative to the perceived location when the eyes were straight ahead. Similarly, perceived touch location was significantly influenced by head position. The perceived location of the touch was displaced in the same direction as the head (F (2,18) = 6.03, P = .01, η_P^2 =.40). A significant effect of

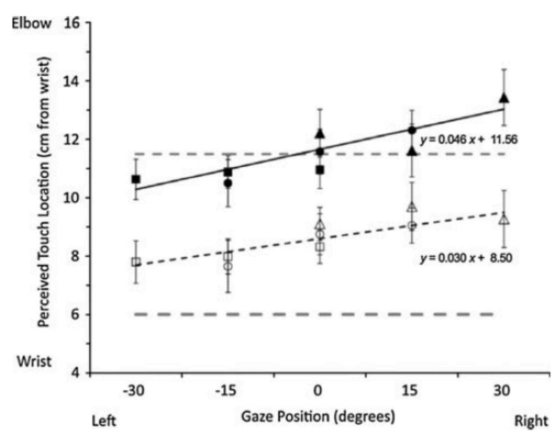

Fig. 2 Effect of gaze position on perceived touch location on the right arm. Data points represent the results for each solenoid for each combination of head and eye position. Data for the eye positions at a particular head position are marked by different symbols (square for head 15 degrees left, circle for head centered, and triangle for head 15 degrees right). Error bars show one standard error of the mean. Regression lines are fitted to the entire data set for each solenoid. The regression equations are indicated on the figure. Dashed gray lines indicate the actual location of each solenoid. Larger numbers for gaze position and perceived touch location indicate positions further to the right and toward the elbow. Gaze shifted the perceived location of touches by 0.38 mm per degree of eccentricity

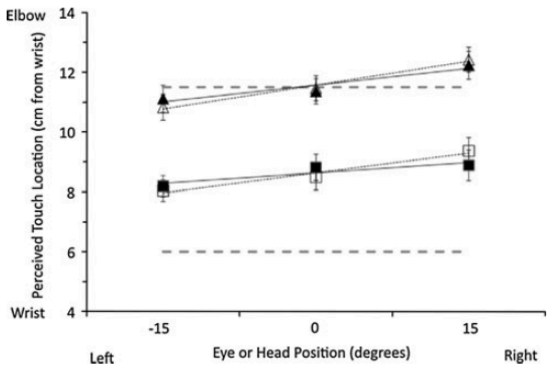

Fig. 3 The effects of eye-in-head (filled symbols) and head-on-body (open symbols) on perceived touch location for the two touch locations (squares and triangles) were similar. Data for eye position were obtained by averaging across head position. Data for head position were obtained by averaging across eye positions. Error bars show one standard error of the mean. Regression lines were fit to the data points shown for the average effect of head and eye position for each solenoid. The effect of eye position was 0.37 and 0.23 mm per degree of eccentricity for solenoids at 11.5 and 6 cm from the wrist, respectively. The effect of head position was 0.53 and 0.44 mm per degree of eccentricity for the same two solenoids. Larger numbers for eye or head position and perceived touch location indicate positions further to the right and toward the elbow

solenoid location (F (1,9) = 79.08, $P < .001$, $\eta_P^2 = .90$) confirmed that perceived touch location was related to the area of skin where the touch was administered and that the two touches could be discriminated. No significant interactions were found, indicating that the effects of eye and head position were independent (F (4, 36) = 0.82, P = .52). Also, the effect of eye (F (2, 18) = 2.70, P = .09) and head (F (2, 18) = 0.14, P = .87) position did not depend on touch location. The three-way interaction was also not significant (F (4,36) = 1.04, P = .40).

A direct comparison of the effects of eye and head positions is presented in Fig. 3, which plots the effects of eye position (collapsed across head position) and the effects of head position (collapsed across eye position) superimposed on each other. The regression lines presented in Fig. 3 show an average effect of +0.30 mm of touch displacement per degree of eye eccentricity and +0.48 mm touch displacement per degree of head eccentricity. If the effects of eye and head positions differ, an interaction of body part and direction of eccentricity should be found. A three-way repeated measure ANOVA was conducted with body part (eye or head), direction of eccentricity (15° left, center, or 15° right), and touch location as factors. The body part by direction of eccentricity interaction was not significant (F (2,15) = 0.17, P = .80). Similarly, no significant effect of body part (head or eye) was found (F (1,9) = 0.13, P = .73). Together, these results indicate that the head and eye effects were not significantly different.

Discussion

The perceived location of a mechanical touch on the arm was found to shift in the same direction as an eccentric eye or head position and by approximately the same amount in each case. The effects were independent of one another and appeared to be linear over the ±15-degree range tested. This is consistent with a gaze signal being used to convert between body and retinotopic coordinates. If a different reference frame were used, gaze position would not be necessary to compute the transform and gaze-related errors would not be expected. This conversion may be done in order to represent tactile and visual locations in the same coordinates.

Our findings add to converging evidence that touch location is coded in an egocentric visual reference frame. Research using transcranial magnetic stimulation indicates that the posterior parietal cortex remaps touch location from body to external or visual coordinates (Azañón et al. 2010; Bolognini and Maravita 2007). Also, blind people appear to code touch location differently from sighted individuals (Röder et al. 2004, 2008), supporting the idea that a visual coordinate system is normally used in tactile coding.

Shift of perceived touch location with head eccentricity

The perceived location of sounds and lights have been found to depend on head position but only one previous study has looked at the effect of head position on the perceived location of tactile stimuli. The head position–related shift we report here is at odds with the results of that study. Ho and Spence (2007) found that the perceived location of a touch indeed shifted related to head position, but in the direction *opposite* to head position. The magnitude of the shift we report is also larger than Ho and Spence observed. The head-related shifts noted in the present study were of the order of +0.48 mm per degree of head eccentricity, whereas data from Ho and Spence yield an effect size of only −0.05 mm per degree.[2]

The difference in the magnitude of effects between the two studies may be partially due to different head displacements. Our head position range was only ±15 degrees, while Ho and Spence (2007) used head positions of ±90 degrees. If head position had larger effects near center but the effect saturated at large head positions, this could lead to the much smaller effect size reported by Ho and Spence. Such a saturation of effects may result because of

[2] Ho and Spence (2007) reported data as numbers between 0 and 1 representing the proportion of distance along a tactor-mounted belt. To calculate the perceived location of touches in cm, we multiplied the numbers reported by 28 cm, the distance between the tactors. Head positions used in the calculation were as reported, ±90 degrees as well as straight ahead.

the physiology of head movements, where only about 50% of the total range of rotation actually result from the head rotating around the top two vertebrae, while the additional 50% of rotation of the head comes from rotations within the spine itself (Fielding 1964). If the signal for head displacement from the head rotation around the spine were subject to systematic errors but the signal related to the rotation of the spine was not, the effect would be expected to asymptote at that rotation.

The pattern of stimulation used is another factor that might contribute to the differences in magnitude in the two studies. Ho and Spence (2007) used vibrotactile stimulation at 250 Hz while we used a 50 ms mechanical depression of the skin. These different types of stimulation are encoded by different touch receptors. Our stimuli would optimally stimulate the slowly adapting Merkel receptors, which are the smallest and most useful receptors for tactile spatial localization. In contrast, the vibrotactile stimulation at 250 Hz used by Ho and Spence would optimally stimulate the very rapidly adapting Pacinian corpuscle receptors, which are most sensitive to vibration and have large diffuse receptive fields. The pathways from these receptors are anatomically distinct from the slowly adapting touch receptor system (Friedman et al. 2004) and may correspond to different cortical maps. Vibration-based maps are likely to be less precise which might explain the smaller effect sizes reported by Ho and Spence.

Another possible explanation for the difference in magnitude might arise from the fact that Ho and Spence (2007) used blocked trials at each head position. Since the head remained at an extreme position for several minutes, adaptation could have occurred causing a shift of perceived straight-ahead toward the current head position. As little as 3 min of eccentric head position has been shown to cause a 10% adaptation in perceived straight ahead (Lackner 1973). This might cause a drastic reduction in the systematic errors caused by the head position signal, possibly even reversing them.

Finally, the body part where touches were administered could contribute to the different pattern of errors found. We applied touches to the skin of the forearm, whereas Ho and Spence (2007) used touches on the torso. It is possible that touches to the arm and the torso are coded in different ways, causing different patterns of errors. Perhaps the visual representation of the torso is left–right reversed (as we are more used to seeing our own torsos in a mirror).

Clearly, more thorough investigation into the effects of eye and head positions on touches stimulating different parts of the body and different receptor types is warranted.

Shift of perceived touch position with eye eccentricity

The eye position–related shift we report here confirms the findings of Harrar and Harris (2009) that eye eccentricity shifts mechanical touches on the arm in the same direction as eye position. The present study showed that eye eccentricity shifted the perceived location of touches by +0.38 mm per degree whereas Harrar and Harris report a figure of +0.68 mm per degree. While both studies used the same single mechanical touch to the same part of the arm with interleaved eye position conditions, there are some differences between the two studies. Harrar and Harris touched the left arm while here the right arm was touched. Differing magnitudes of effect could reflect an asymmetry related to arm dominance; perhaps the right arm has touch coded more accurately compared to the left. Also, the method of response was different. In the study by Harrar and Harris, participants respond by reading the location of perceived touch off a ruler placed adjacent to the touch box. The eyes scanned the ruler and were not returned to a central position during the reporting. It is therefore possible that there were effects of eye position on the perceived position of the probe (ruler) as well as on the touch, thus magnifying the apparent effect. In the present study, the eyes were returned to center before responding and the more psychophysically robust PEST method was used.

Shift of perceived touch position with attention

An alternative explanation for our results is that perceived touch position is shifting with attention, rather than specifically due to eccentricity of the eyes and head. This hypothesis was tested by Harrar and Harris (2009). They had had participants maintain a centered eye and head positions while an LED flashed eccentrically diverting participant's attention in that direction. Participants received a touch on their arm while their attention was diverted and then indicated the location of the touch. The perceived location of the touch was found to shift in the direction of attention but accounted for only about 17% of the effect of eye position. We expect that attention played a similar role in the present experiment and contributes only a small amount to the magnitude of shift we report.

Localization accuracy

While the perceived position of the touch closer to the elbow was accurate when fixating straight ahead, the touch closer to the wrist was always shifted toward the elbow as can be seen in Figs. 2 and 3. The pattern of touch being perceived as closer to the elbow is consistent with other findings that touches on the forearm are perceived proximally to their actual location (Cody et al. 2008).

Are conversions to head and retinal coordinates done in series or parallel?

The systematic errors in perceived location of touch due to eccentric eye and head positions reflect systematic underestimations that are made when accounting for eye and head positions during the reference frame conversion. How these conversions are accomplished is not well understood. It could be that the eye and head positions are accounted for separately, both causing small, independent effects on perceived touch location, reflecting a sequential conversion from body to head to retinal coordinates. Alternatively, eye and head positions could be combined into a gaze signal at an earlier stage of processing, so that only the position of gaze is needed to convert touch location into a visual reference frame. The superior colliculus codes desired gaze in a single signal, with contributions of head and eye position accounted for downstream (Freedman and Sparks 1997; Klier et al. 2001). Our data suggest that the neural code used in tactile-to-visual coordinate transformations uses a single gaze signal of that type, rather than individual signals for eye and head positions.

Conclusion

Gaze eccentricity caused a shift in perceived tactile localization. The effect was the same whether it was due to eye or head displacement. This supports of the idea that touch location is transformed into retinotopic coordinates and that a gaze signal is used to compute the transformation.

Acknowledgments This project was sponsored by a grant from the Natural Sciences and Engineering Research Council (NSERC) of Canada to LRH; LMP is sponsored by NSERC Collaborative Research and Training Experience Program (CREATE).

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Appendix D: Pritchett, Carnevale & Harris 2012

Pritchett, L. M., Carnevale, M. J., & Harris, L. R. (2012). Reference frames for coding touch location depend on the task. *Experimental Brain Research*, *222*, 437–445. doi:10.1007/s00221-012-3231-4

Exp Brain Res (2012) 222:437–445
DOI 10.1007/s00221-012-3231-4

RESEARCH ARTICLE

Reference frames for coding touch location depend on the task

Lisa M. Pritchett · Michael J. Carnevale · Laurence R. Harris

Received: 17 July 2012 / Accepted: 11 August 2012 / Published online: 1 September 2012

Abstract The position of gaze (eye plus head position) relative to body is known to alter the perceived locations of sensory targets. This effect suggests that perceptual space is at least partially coded in a gaze-centered reference frame. However, the direction of the effects reported has not been consistent. Here, we investigate the cause of a discrepancy between reported directions of shift in tactile localization related to head position. We demonstrate that head eccentricity can cause errors in touch localization in either the same or opposite direction as the head is turned depending on the procedure used. When head position is held eccentric during both the presentation of a touch and the response, there is a shift in the direction opposite to the head. When the head is returned to center before reporting, the shift is in the same direction as head eccentricity. We rule out a number of possible explanations for the difference and conclude that when the head is moved between a touch and response the touch is coded in a predominantly gaze-centered reference frame, whereas when the head remains stationary a predominantly body-centered reference frame is used. The mechanism underlying these displacements in perceived location is proposed to involve an underestimated gaze signal. We propose a model demonstrating how this single neural error could cause localization errors in either direction depending on whether the gaze or body midline is used as a reference. This model may be useful in explaining gaze-related localization errors in other modalities.

Keywords Tactile localization · Reference frames · Head · Gaze · Body representation · Posture

L. M. Pritchett · M. J. Carnevale · L. R. Harris
Centre for Vision Research, York University, Toronto, ON, Canada

L. M. Pritchett (✉)
Department of Psychology, York University, Toronto, ON M3J 1P3, Canada
e-mail: lmpritch@yorku.ca

Introduction

The multiple sensory modalities contribute spatial information each in a unique reference frame. Visual stimuli are initially coded in retinal coordinates, tactile stimuli relative to the skin surface, and auditory stimuli relative to the head. These initial representations of stimulus location are constrained by the anatomy of sensory receptors and need to be converted to other reference frames to provide perceptually useful information such as location in space. Higher levels of processing combine information arising from different sensory modalities into a single coordinate system or else some hybrid system of multiple simultaneous reference frames (Andersen et al. 1993; Cohen and Andersen 2002; Colby 1998; Deneve and Pouget 2004). Previous studies have suggested that a gaze-based reference frame may be the most likely candidate (Azañón et al. 2010; Bolognini and Maravita 2007; Harrar and Harris 2009, 2010; Knudsen and Knudsen 1985; Röder et al. 2004, 2008).

If stimuli are coded relative to gaze, then a gaze signal is required to transform the location from the reference frame of the end organs to the central representation. Any systematic errors in coding the position of gaze would, therefore, shift the perceived location of stimuli. Indeed, several authors have demonstrated that eye position is underestimated (Harris and Smith 2008; Hill 1972; Morgan 1978) and corresponding systematic errors in localizing various stimuli have been reported related to eye position (auditory: Lewald and Ehrenstein 1996a, b; Weerts and Thurlow 1971; visual: Bock 1986; Fiehler et al. 2010; Henriques et al. 1998; Lewald 1998; tactile: Harrar and Harris 2009, 2010). Similarly, eccentric head orientation has also been found to produce errors in localizing auditory (Lewald and Ehrenstein 1998; Lewald et al. 2000; van Goossens and Opstal 1999), visual (Kopinska and Harris 2003; Wexler 2003), and tactile stimuli (Ho and Spence 2007; Pritchett and Harris 2011).

The effects of eye and head position on tactile (Pritchett and Harris 2011) and auditory (Lewald and Ehrenstein 1998) localization are equivalent. This equivalency suggests that head and eye position may be combined into an encompassing gaze signal that may then form the reference for spatial locations. This is consistent with research showing that several monkey cortical and subcortical areas use a single signal for gaze where eye and head information is combined (Martinez-Trujillo et al. 2003).

Although it is known that stimuli are systematically mislocalized when gaze is eccentric, there are inconsistent reports on the nature and direction of these localization errors. In auditory perception, most reports are of perceived locations shifting opposite to eccentric eye or head position (van Goossens and Opstal 1999; Lewald and Ehrenstein 1996a, 1998; Lewald 1998; Lewald et al. 2000) although there are some reports of the perceived location of auditory targets shifting in the same direction as gaze (Lewald and Ehrenstein 1996b; Weerts and Thurlow 1971).

Most pertinent to the current study are the contrasting directions of tactile mislocalization found in response to head position. Ho and Spence (2007) reported that when participants localized vibrotactile stimuli presented on the waist while holding an eccentric head orientation, tactile localization was biased in the direction opposite to head position. In contrast, results from this laboratory have demonstrated that brief touches presented on the forearm were mislocalized in the same direction as eye (Harrar and Harris 2009, 2010) and head position (Pritchett and Harris 2011). The current study was therefore conducted to resolve this discrepancy.

Comparing the studies on tactile localization errors related to head position (Ho and Spence 2007 vs. Pritchett and Harris 2011) is not straightforward as the studies differ along important dimensions. First, different types of touch stimuli were used and thus different sensory pathways could potentially lead to differences in the subsequent position coding. Ho and Spence (2007) used vibrotactile stimuli at 250 Hz which are primarily detected by the deep layer Pacinian corpuscles that have large receptive fields (Jänig et al. 1968). Pritchett and Harris (2011) used brief discrete solenoid touches that are detected primarily by surface layer Merkel receptors with receptive fields substantially smaller than Pacinian corpuscles (Johansson and Vallbo 1979). There is evidence that information from these different receptor types may be coded in different cortical maps (Friedman et al. 2004) that may underlie the different results reported using these different tactile stimuli. Second, Ho and Spence (2007) tested tactile localization on the front of the waist while Pritchett and Harris (2011) tested the forearm. These two body parts utilize different body landmarks as tactile reference frames, which may lead to unique localization biases (Cholewiak and Collins 2003 for abdomen, Cholewiak 2004 for forearm). Finally, in addition to type and place of stimulation, the studies used different experimental procedures. Different task demands could lead to different location-encoding mechanisms. In the study by Ho and Spence (2007) participants both received stimuli and made their responses while their heads were eccentrically positioned, while Pritchett and Harris (2011) had participants return to straight ahead before responding.

We first replicated and extended the Ho and Spence (2007) studies using the same kind of stimulation (250 Hz vibration) and body part (torso) with the participants both receiving stimuli and making responses with an eccentric head position. In Experiment 2, we used the same stimuli and body part but a protocol similar to that of Pritchett and Harris (2011) where participants received tactile stimuli in an eccentric head position but returned to center before responding. Results indicated that it was the type of task that determined the direction of localization errors and ruled out the other possible factors listed above.

Experiment 1 and 2 method

Participants

Eight participants (4 male, 4 female, mean age 28 years) volunteered to participate in Experiment 1. Experiment 2 had eight participants (4 male, 4 female, mean age 31 years), six of whom also participated in Experiment 1. All reported having a normal sense of touch and normal or corrected-to-normal vision. All experiments were approved by the ethics board of York University and followed the guidelines of Helsinki.

Apparatus

The vibrotactile stimuli were presented using an array of eight tactors (Model C2, Engineering Acoustics, Florida, USA) for all experiments. The tactors were mounted on a belt worn around the participant's waist. The eight-tactor array was centered on the participant's belly button with the center of each tactor 4 cm from the next. The vibrotactile stimuli were at 250 Hz and were of 50 ms duration. The intensity of each touch was randomly chosen from four possibilities (37.5, 50, 62.5, or 75 % of maximum intensity) in order to keep participants from distinguishing the tactor locations by learning any subtle differences in their intensities.

Head and eye position were manipulated by fixation points positioned in space and a laser mounted on a hat worn on the participant's head. During testing participants were seated in a darkened room in a chair chosen for its high supportive back extending above the head. Participants maintained a seated upright posture in all experiments. Each experiment used a slightly different set up of chair position and fixation points to facilitate the different experimental procedures (see Fig. 1). The details specific to each procedure are described below.

A 21-inch LCD computer monitor was used to display a visual scale (described below) for recording the perceived location of touches and to display fixation points. For all experiments, the computer monitor was 55 cm from the viewer when the visual scale was presented. Participants used a cordless optical mouse to indicate the perceived location of the touch on the scale.

Visual scale for reporting perceived touch location

Before beginning each experiment, the vibrotactile stimuli were delivered from each tactor in order from the furthest right to the furthest left. Participants were instructed to memorize the location of the end points of the array and to use the end points of a white bar ($35.3° \times 0.62°$ visual angle) presented on the screen to represent those locations (as in Ho and Spence 2007). Participants reported the perceived location of touches by moving a sliding bar ($0.51° \times 0.77°$ visual angle) along the scale by means of a mouse. The bar could be moved by dragging it, by clicking on the desired location on the scale, or by clicking the left or right spaces at the end of the scale. When the participant was happy with the positioning of the vertical bar they clicked on an "OK" button at the bottom of the screen. This response method is the same as used by Ho and Spence (2007).

The unique details for each experiment are described below.

Experiment 1

The first experiment was a replication of Ho and Spence (2007). One change from their protocol was the use of the head laser to enable participants to reliably position their heads in all conditions. Participants were arranged with their head either 90° left, 90° right or straight with the screen straight ahead of them (Fig. 1). Each trial began with a fixation cross displayed centered on the screen, the head-mounted laser was illuminated and the participant fine adjusted their own head position. This was done to make the conditions as similar as possible between all the experiments. After 2 s the fixation cross and laser were turned off and a vibrotactile stimulus was presented from a randomly chosen tactor along the array. The visual scale was displayed on the screen 500 ms later and the participant indicated the perceived location of the touch. Clicking the "OK" button led to the beginning of the next trial. Each of the eight tactors was presented 12 times which took about 7 min. Once the block was complete, the experimenter moved the chair into the next position (see Fig. 1) and the next block of trials commenced until all three head conditions had been run. Running order was counterbalanced across participants.

Experiment 2

The second experiment followed a procedure similar to Pritchett and Harris (2011) but with the vibrotactile stimulation on the torso and the response measure (the visual scale) that was used by Ho and Spence (2007). The chair was positioned so that the participant looked at the computer monitor with their head and eyes straight ahead. Target LEDs to indicate required eye and head position were positioned 90° to the left and 90° to the right of the participant.

Each trial began by directing the participant to the fixation position for that trial. If it was a head-centered trial, the fixation cross on the screen was presented. If it was a left or right head condition trial, an arrow was displayed on the screen pointing in the appropriate direction, left or right. The participant was given 2 s to turn their head to the specified direction and to align their head-mounted laser to the illuminated LED at 90°. After 2 s the fixation point was removed, the head laser turned off, and the vibrotactile stimuli were presented from a randomly chosen location on the tactor array. The head laser then turned on again and the participant turned their head back to align the laser with a centered fixation point before reporting the location of the touch on the visual scale. The next trial began when they clicked the "OK" button. Each of the eight tactors was presented 12 times for each head condition for a total of 288 trials. The experiment was approximately 21 min in duration.

Data analysis

Participants reported the perceived location of touches on a linear scale. The furthest left end was coded as 0, and the furthest right end was coded as 1. Data were transformed into cm from navel by multiplying by 28 cm, the distance

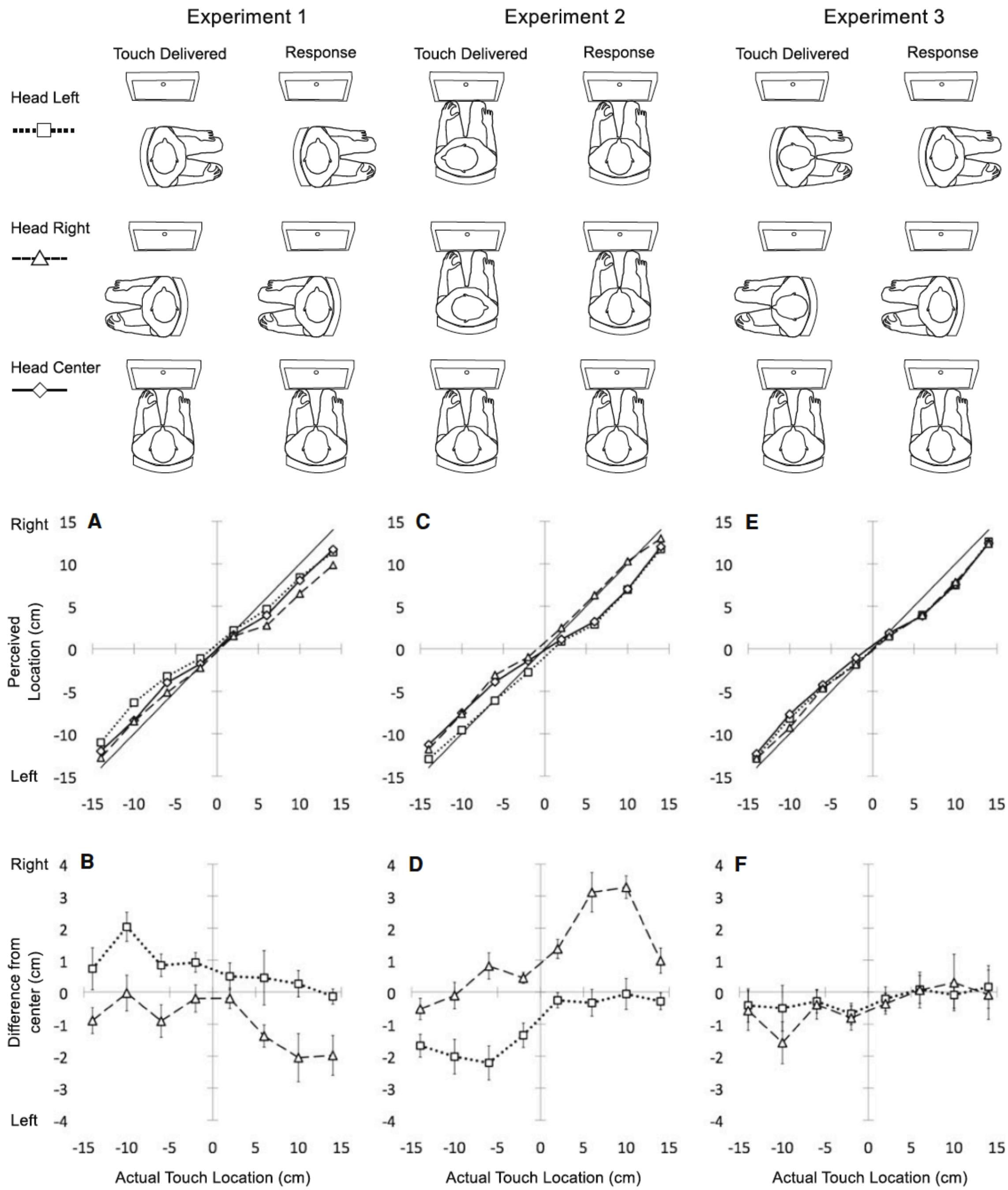

Fig. 1 Head and body positions during touch delivery and response are illustrated for each experiment. In Experiment 1, head position was manipulated in a blocked design as in Ho and Spence 2007, the head was eccentric for touch delivery and during reporting perceived touch location. In Experiment 2, head position was manipulated in a randomized design, and the head was always returned to the center to report touch location. In Experiment 3, the touch was always delivered with head centered and the head then turned before responding. In **a**, **c** and **e** perceived locations (related to the body midline at 0) of the 8 tactors under head left (*dotted line, square symbol*), head right (*dashed line, triangle symbol*) and head center (*solid line, diamond symbol*) are shown for each of three experiments. Standard *error bars* are the size of the *symbols*. In **b**, **d** and **f** the difference between the head-eccentric and head-centered locations are illustrated for the three experiments. *Error bars* show one standard error of the mean

between the first and last tactor and subtracting 14. For each participant the mean reported position for each touch location at each head position was averaged over 12 trials. This perceived location data were subjected to a two-way repeated-measures ANOVA. The effect of head position was quantified by calculating the difference between the perceived location of a touch during the eccentric head condition and the perceived position of the same touch during the centered head condition. This absolute difference from center data was used as an index of the magnitude of the effect of head position. It was also subjected to a two-way repeated-measures ANOVA for each of the three experiments.

Experiment 1 and 2 results

Experiment 1

The mean perceived location of touch with the head held eccentric is plotted in Fig. 1a. A significant effect of touch location ($F\,(7, 49) = 248.67, p < 0.001$) confirmed that the touch locations could be discriminated. A main effect of head position was also found ($F\ (2,\ 14) = 15.92$, $p < 0.001$) indicating that the perceived position of a touch was influenced by head position. A trend analysis indicated that the effect of head position was linear ($F\,(1, 7) = 25.06$, $p = 0.002$), meaning that left and right head position affected touch location similarly in magnitude but in opposite directions. Touches were perceived furthest to the left in the right head condition ($M = 1.03$ cm left), more medially in the centered head condition ($M = 0.12$ cm left), and furthest to the right in the left head condition ($M = 0.60$ cm right). There was not a significant interaction of head position and touch location ($F\,(14, 98) = 1.45$, $p = 0.147$).

Further analysis of the effect of head position was conducted using the difference between the perceived position of each touch during the head-eccentric trials (left or right) and the perceived position of the same touch during the head-centered trials (Fig. 1b). The average unsigned difference between eccentric and centered head position was used as an index of the magnitude of the effect of head position. These data were subjected to a two-way repeated-measures ANOVA. The main effect of head position was not significant ($F < 1$, ns), indicating that left and right head position effect touch location similarly in magnitude. Additionally, the touch location main effect was not significant ($F\ (7,\ 49) = 2.23$, $p = 0.11$), suggesting that the magnitude of the effect was the same across touch locations. However, a significant interaction of touch location by head position was found ($F\ (7,\ 49) = 5.75$, $p = 0.013$). As can be seen in Fig. 1b, head position had a larger effect on touches that were located on the same side of space. Thus, when the head was positioned to the left the touches on the left were affected more ($M = 11.3$ mm left tactors, $M = 6.0$ mm right tactors) and when the head was positioned to the right the touches on the right were affected more ($M = 16.0$ mm right tactors, $M = 8.7$ mm left tactors).

We hypothesized that holding the head eccentrically for several minutes might lead to some kind of adaptation, which might affect the coding of touch location. Therefore, we calculated correlations between the perceived position of touch and the time in seconds since the participant had began that head condition. Pooling across and controlling for touch location, no evidence for a drift in perceived position of touch was found for either left ($r\ (766) = -0.009$, $p = 0.80$) or right ($r\ (766) = 0.055$, $p = 0.13$) head positions.

Experiment 2

The localization data from Experiment 2 where the head returned to center before the response was made is plotted in Fig. 1c. These data were analyzed using a two-way repeated-measures ANOVA. A significant effect of tactor location ($F\ (7,\ 49) = 244.83$, $p < 0.001$) confirmed that touch location could be discriminated. A significant effect of head position ($F\ (2,\ 14) = 17.36$, $p = 0.004$) indicated that the perceived position of a touch was affected by head position. As in Experiment 1, the effect of head position was found to be linear ($F\ (1,\ 7) = 17.82$, $p = 0.004$), indicating that left and right head positions affected perceived touch location equally in magnitude but opposite in direction. Touches were perceived furthest to the left when the head was positioned to the left ($M = 1.13$ cm left), more medially when the head was centered ($M = 0.11$ cm left), and to the right when the head was right ($M = 1.06$ cm right). A significant interaction of head position by touch location was found ($F\ (14,\ 98) = 8.57$, $p < 0.001$), indicating that the effect of head position was different at the different touch locations. This effect is further explored in the analysis of the difference-from-center data (Fig. 1d).

The unsigned difference data were subjected to the two-way repeated-measures ANOVA. The main effect for head location was not significant ($F\ (1,\ 7) = 2.31$, $p = 0.17$), indicating that the size of the head orientation effect was equal for the left ($M = 1.14$ cm) and right ($M = 1.34$ cm) head orientations. A main effect of tactor location indicated that the effect of head position was different depending on the location of the touch ($F\ (7,\ 49) = 6.29$, $p = 0.003$). The head position by touch location interaction was also significant ($F\ (7{,}49) = 9.062$, $p = 0.002$). This indicated that touches on the same side as the eccentric head position were affected more (head left, left touches $M = 1.62$ cm; head right, right touches $M = 1.94$ cm) than those on the opposite side (head left, right touches $M = 0.66$; head right, left touches $M = 0.74$ cm).

Experiment 1 and 2 discussion

The results of Experiment 1 replicate Ho and Spence (2007), showing that when touches are localized under eccentric head conditions the perception is shifted in the opposite direction of head eccentricity. The results of Experiment 2 are consistent with the results of Pritchett and Harris (2011), demonstrating that when a touch is applied under eccentric head position but reported under centered head position the perception is shifted in the same direction of head eccentricity.

We can therefore conclude that the opposing results are not due to the different body parts tested (torso vs. arm) or to the type of touch stimuli used (vibration or tap). We can also rule out adaptation affects during the blocked head condition trials of Experiment 1 as no systematic drift in perceived touch location was found across time.

Other differences between the two procedures are that the scale used for response in Experiment 1 was viewed with the head-eccentric and that it was necessary to remember and update the location of the touch after moving the head in Experiment 2. Experiment 3 was therefore designed to test the possible contribution of these two factors. In Experiment 3, touches were delivered while the head was centered, but the response was made with head-eccentric; thus, the scale was viewed with head-eccentric (as in exp 1), and it was necessary to remember the location of the touch during a movement (as in exp 2), but the touches were delivered with the head and eyes centered.

Experiment 3

Participants

Eight participants (4 males, 4 females, mean age 28 years) completed Experiment 3. Five of them had also completed both Experiments 1 and 2.

Method

Participants were arranged with their body pointing either to the left, right, or straight toward the screen for each block of trials. In conditions where the participant was not facing the monitor, an LED was placed directly in front of the participant as a fixation point; when facing the monitor, a cross displayed on the screen was used. To begin each trial the central fixation point and the head-mounted laser were illuminated and participants aligned their eyes and head with this point. After 2 s the fixation and head-mounted laser were turned off, and a touch was presented from a randomly chosen tactor on the array. Next, the laser and a fixation cross on the computer monitor were illuminated. Participants were given 2 s to align the head laser with the fixation cross. Next the visual scale was displayed on the screen. The participant reported the perceived location of the touch on the scale and clicked the "OK" button. This triggered the beginning of the next trial. The participant turned their head back to the centered location and aligned the laser and their eyes with the fixation point ready for the next trial. Each of the 8 tactors was presented 12 times before the block terminated in approximately 7 min. The chair was then repositioned, and the next head condition was run until all three had been completed. Conditions were counterbalanced across participants.

Results

The localization data from Experiment 3 are plotted in Fig. 1e, f and were analyzed using a two-way repeated-measures ANOVA. The main effect of touch position was significant ($F\,(7, 49) = 539.10$, $p < 0.001$), indicating that the touches could be discriminated. The main effect of head position was not significant ($F\,(2, 14) = 2.56$, $p = 0.12$), indicating that the touches were perceived similarly regardless of the position of the head at the time when the location was reported. Finally, the touch location by head position interaction was not significant ($F\,(14, 98) = 0.77$, $p = 0.54$). These results indicate that there was no effect of head position on the response. This suggests that there were no effects of eccentrically viewing the scale in Experiment 1 or of moving the head in Experiment 2.

General discussion

The experiments described here confirm that there is a systematic effect of head position on perceived touch location and that this depends critically on the procedure used to measure it. We have successfully reproduced the effect of shifting touch in the opposite direction of eccentric head position when following the procedure of Ho and Spence (2007). And we replicate the effect of shifting perceived touch location in the same direction as head position when following procedures more similar to Pritchett and Harris (2011).

The present experiments allow us to rule out some explanations for the opposing effects. The difference is not

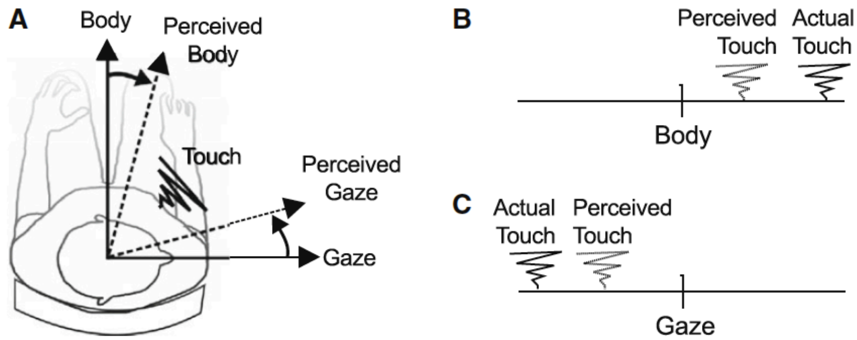

Fig. 2 Model of how an eccentric head position may shift perceived touch location in either the same or opposite direction as head position. *Solid lines* represent accurate locations, *dashed lines* represent perceived locations (of body and gaze in **a** and of touch in **b**, **c**). **a** Illustrates different consequences of an underestimated gaze angle. The perceived body center is shifted toward gaze and perceived gaze is shifted toward the body (see text for details). **b** The result of coding relative to a shifted body midline is that the perceived location of touch is shifted in the direction opposite to head position. **c** The result of coding relative to a shifted gaze direction is that the perceived location of touch is shifted in the same direction as head position

simply due to type of touch (vibration or tap) or to the body part tested (torso vs. arm). We can rule out adaptation effects during the blocked head condition trials of Experiment 1 as no systematic drift in perceived touch location was found across time. Finally, the null results of Experiment 3 demonstrate that the difference cannot be simply explained as resulting from eccentric viewing of the scale in Experiment 1, or from moving the head in Experiment 2. Instead, the results point to different mechanisms for encoding, storing, or retrieving touch location in the two experimental situations.

Lewald and Ehrenstein (1996a) argued that auditory localization was only found to move in the direction opposite to gaze when a visual reference was used and that the effect of gaze on visual localization was larger than it was on auditory. This combination can, therefore, make it appear as if auditory localization is shifted in the same direction as gaze because of the opposing effects of gaze on the sound stimulus and on the visual reference used to measure it. Our control study rules out effects of the probe scale as an important contributor to the results reported here. We offer another explanation for opposite effects of gaze on the perceived location of touches in different situations.

Why are gaze-induced localization errors found in opposing directions?

Holding the eyes eccentrically shifts the perceived body straight ahead in the same direction as the eyes (Harris and Smith 2008; Hill 1972; Morgan 1978). Similar results have also been found when the head rather than the eyes is held eccentrically (Yamaguchi and Kaneko 2007). That is, the angle between the body and eye straight ahead is underestimated. As shown in Fig. 2a, an underestimated representation of gaze eccentricity can be described as perceiving the body straight ahead as shifting toward gaze, that is, in the same direction as head position (as in Hill 1972 Experiment 2 and 3). Or, it may be regarded as the location of gaze moving closer to the actual body, that is, a shift in the direction opposite to head position (as in Hill 1972 Experiment 4). Thus, which direction the perceived touch location shifts may be dependent on the frame of reference (body or gaze) to which it is attached.

As shown in Fig. 2b, if the body midline were shifted in the same direction as head position, any location coded relative to body midline would show errors in the direction opposite to head position. In contrast, Fig. 2c shows that if perceived gaze were shifted in the opposite direction of head position, then any stimuli coded relative to gaze would show errors in the same direction as eccentric position. We therefore conclude that the opposing effects of gaze eccentricity described here may be the result of coding stimuli relative to the body in Experiment 1 and relative to gaze in Experiment 2.

This explanation is consistent with work in the auditory domain. Numerous reports exist of auditory perception shifting in the direction opposite to gaze (Kopinska and Harris 2003; Lewald and Ehrenstein 1996a, b, 1998). The explanation offered for this shift has been that it is linked to a shifted perceived median of the head. When participants were asked to adjust a dichotic sound until it sounded as if it were in the middle of the head while their eyes (Lewald and Ehrenstein 1996a, 1998) or head (Kopinska and Harris 2003; Lewald and Ehrenstein 1998) were turned, participants consistently adjusted the sound such that it was more intense in the ear on the same side as gaze. This indicated that they perceived the sound as shifted in the direction opposite to gaze.

Mechanism

Touch location is initially coded by a labeled-line system where the nerve endings in the skin transmit information to the primary somatosensory tactile homunculus. If the conscious perception of touch arose from that representation, then no systematic errors related to gaze position would be expected: perceived touch location should correspond directly to actual touch location. However, the parietal cortex contains many spatial representations that are responsive to tactile as well as visual and auditory stimulation (Avillac et al. 2005; Cohen and Andersen 2002; Galati et al. 2001; Mullette-Gillman et al. 2005; Schlack et al. 2005). These multisensory maps are thought to code space in different coordinate systems. For example, the lateral intraparietal area (LIP) of the monkey seems to code space not only in an eye-centered representation but also relative to head-centered and intermediate reference frames (Mullette-Gillman et al. 2005; Stricanne et al. 1996), while the ventral intraparietal area (VIP) seems to code space in a body-centered representation (Sereno and Huang 2006). Converting touch information from a body representation into head, eye, or gaze frames requires taking eye and head position into account. Inaccuracies in the representation of head, gaze, or eye position thus get passed along as tactile space is converted into such a frame.

Why are our effects asymmetrical?

A noticeable feature of our data is the asymmetry of the effects on the left and right sides of the body (Fig. 1b, d). When the head was turned to the left the touches on the left side of the body were more affected, and when the head was turned to the right the touches on the right side of the body were more affected. This is true for both Experiment 1 and 2 as can be clearly seen in the data of Fig. 1a, b. It seems that only the touches on the same side of the body as the direction of gaze are affected. When interpreted in the context of the frame conversion model, this might suggest that only touches within the current visual field are recoded relative to the body midline or gaze. The non-affected touches, which are outside the visual field, may remain coded in the original somatotopic reference frame. This is consistent with other work showing that vision affects coding of touch location (Haggard et al. 2007; Kennett et al. 2001; Sathian and Zangaladze 2002; Tipper et al. 2001). Another possibility is that touches on the side of the body opposite to gaze are coded in both gaze- and body-centered coordinates simultaneously with equal weighting. In that case, the opposite-directed errors could cancel out.

Conclusion

The results of the experiments described here suggest that perceived locations of tactile stimuli are coded differently depending on the situation. In the static design of Experiment 1 and Ho and Spence (2007), touch location may be coded relative to the body, while in the more dynamic conditions of Experiment 2 and Pritchett and Harris (2011), touch may be coded relative to gaze. This may be connected to using a more centralized, gaze-centered reference frame when the locations of touches need to be remembered and reconstructed after a move. These findings may have important applications in designing working environments as spatial representations may be different depending on context and task demands. Drivers, pilots or users of backhoes, for example, may interpret the location of tactile objects differently depending on the situation and where they are looking. These findings may improve our understanding of the different patterns of spatial neglect that are seen in parietal brain damage patients attempting different tasks (see Colby 1998) and may have implications for the blind.

Acknowledgments This research was funded by a Discovery Grant to Laurence Harris from the Natural Sciences and Engineering Research Council of Canada.

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